IMPACT OF THE INTRODUCED NEW ZEALAND SCREWSHELL *MAORICOLPUS ROSEUS* ON SOFT-SEDIMENT ASSEMBLAGES IN SOUTHEAST TASMANIA

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Submitted in fulfillment of the requirements for the Degree of Doctor of Philosophy (Quantitative Marine Science)

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JUNE 2010

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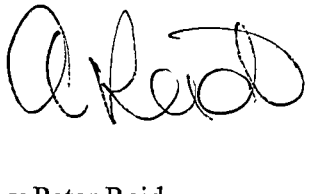

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ABSTRACT

Non-indigenous species (NIS) continue to have major impacts on the integrity, diversity and health of native terrestrial, freshwater and marine ecosystems globally. The New Zealand Screwshell (*Maoricolpus roseus*) is a turritellid gastropod inadvertently introduced to Tasmania during the 1920s. It has since become one of Australia's most widespread marine invasive species, occupying vast areas of benthic habitat along Australia's SE coast. In Australia, *M. roseus* occupies a range of habitats from muddy silts to rocky reef although it is most common on shelly substrates and course sands over a depth range of 0 - 200 m, and regularly attains densities of 600 - 2500 m^{-2}. Given that *M. roseus* has occupied vast areas of sea floor at high densities for extensive periods of time, the potential exists for this species to invoke large ecological changes to its recipient communities. Despite this, the impact of the screwshells is yet to be either qualitatively or quantitatively examined.

Due to the absence of baseline data on the abundance and distribution of native species prior to the arrival *M. roseus ca.* 90 years ago, assessing impacts of the species using a before-after comparison was not possible. In this study I employed a combination of qualitative surveys and *in situ* manipulative experiments at a variety of spatial, temporal and conceptual scales in order to develop a robust quantitative assessment of the impact of *M. roseus*. This approach involved employing several independent assessments of impact: (a) experiments in which impacts of *M. roseus*

to community structure are assessed and separated; (b) experiments in which impacts of *M. roseus* to benthic community function are quantified using *in situ* metabolic chambers; (c) quantitative surveys which examine the relationship between screwshells and commercially important scallop species; and (d) experiments in which the impacts of *M. roseus* on growth and development of commercially important scallops are assessed. Importantly, the experimental and survey designs used were developed to address two unique facets. Firstly, the design of the experiments and surveys allowed identification of the spatial and temporal variability of *M. roseus'* impacts. Secondly, the designs allowed for quantification of the separate impacts of *M. roseus* on the structure and function of native soft-sediment communities.

In the D'Entrecasteaux Channel (SE Tasmania) where *M. roseus* is known to be patchily distributed at a range of densities from 0 - 2000 m^{-2}, *in situ* experiments clearly demonstrated a marked impact on the structure and metabolism of the benthic community due to the presence of the screwshells. Typically, communities associated with high densities of screwshells exhibited elevated species richness and abundances of total macroinvertebrates when compared to patches of benthos with low densities of screwshells, and areas devoid of the species. Further, such communities exhibited significantly higher metabolic rates (both respiration and production), although the specific metabolic rates fundamentally depended upon whether screwshells were alive, dead and empty, or supporting hermit crabs.

Observations from surveys combined with *in situ* experiments also highlighted impacts of *M. roseus* on commercial species. The distribution of three native scallop species in the D'Entrecasteaux Channel depended upon the distribution and density of *M. roseus*, in addition to the coarseness of the sediments. Further, *Pecten fumatus*, the most common of the scallop species, actively avoided areas of benthos supporting screwshells at densities > 200 m^{-2}. Caging experiments also revealed that the condition, growth and weight of *P. fumatus* were significantly impacted by the presence of *M. roseus*.

I collate and interpret the results from *in situ* experimental manipulations and large and small scale surveys to provide a robust estimate of the immediate and potential impacts of *M. roseus* on native soft-sediment ecosystems and commercially important species. The results have highlighted the importance of using multiple methodologies when assessing impacts of NIS, as undoubtedly the most robust information is attained through the use of multiple independent assessments of impact. There is clear evidence that *M. roseus* has drastically altered the structural complexity and integrity of recipient soft-sediment benthic habitats, and the structure and function of the community it supports. Given the magnitude of impact of *M.* roseus on native communities and commercially important species, there is a clear need for a management strategy to be developed for this species. Not only is *M. roseus* a potential threat to the integrity and natural function of native soft-sediment communities, but it is also has the potential to put important recreational and commercial scallop fisheries in Tasmania at risk.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my supervisors Craig Johnson and Jeff Ross for their support, enthusiasm and encouragement throughout the project. You were both an inspiration to me for which I will be forever grateful.

I extend a huge thank you to my family, Mum and Dad, Simon and Lisette for their continual encouragement and emotional support for all these years, despite being so far away. You have always encouraged me not to settle for less than my dreams and compelled me through, particularly during the tough times.

To my fiancée, Karen, whose love and support for all these years has been nothing short of amazing. You have been my rock, encouraged me to chase a dream and aspire to great things in life. You stood by me throughout, the great times and the tough, and I am forever indebted to you. I don't know where I would be without you and I can't wait to share more time with you.

This project could not have been possible without the assistance of friends and co-workers at the School of Zoology. I thank Richard Holmes for his tireless effort in the workshop building various devices and his assistance in the field. Thanks for a great laugh too on those sunny days down the 'Channel'. I also wish to extend my thanks to Christopher 'Kit' Williams for his amazing work on the electronics

associated with the metabolism chambers. Without you, I doubt the project would have succeeded.

I can't begin to thank the cast of thousands who assisted me in the field, and in particular: Adam Stephens, Scott Ling, Tom Sloane, Simon Talbot, Regina Magierowski, Rick and Jemina Stuart-Smith, Tobias Probst, Antonia Cooper, Hugh Pederson. Special thanks must also go to Jemina Stuart-Smith for her tireless effort in sorting samples.

This thesis would also have not been possible without close friends in the Zoology Department: Jemina and Rick Stuart-Smith – thanks immensely for all the cuppas and providing yourselves as sounding boards for ideas; Scott Ling – thanks for your help and advice; Regina Magierowski – thanks for your words of wisdom and all your helpful advice along the way; Paulo Duharte – thanks for always providing a laugh; the CRJ Marine Ecology Lab – especially Jess Melbourne-Thomas for making life in the lab all the more enjoyable.

I also extend thanks to Sue Jones, Sherrin Bowden, Felicity Walsh, Burry Rumbold, Kate Hamilton, Wayne Kelly, Randy Rose, Ashley Edwards, Rob White for making life around the Zoology Department easier, and also a fun place to work.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. NON-INDIGENOUS SPECIES

Human-mediated introductions of non-indigenous species (NIS) continue to be regarded as major threats to the integrity, diversity and health of natural marine and estuarine ecosystems globally (Carlton et al. 1990, Carlton & Geller 1993, Carlton 1996b, a, Cohen & Carlton 1998, Parker et al. 1999, Ruiz et al. 1999, Ruiz et al. 2000, Crooks 2002, Ross et al. 2003b, a, Ruiz & Hines 2004). In some instances, the impact on recipient marine communities from the invasion of NIS has been extreme, as illustrated in the invasion of San Francisco Bay by the Asian clam *Corbula amurensis* (Carlton et al. 1990, Nichols et al. 1990), the spread of the ctenophore *Mnemiopsis leidyi* throughout the Black and Caspian Seas (Shiganova 1998, Kideys 2002) and the arrival of *Corbula gibba* in Port Phillip Bay, Australia (Currie & Parry 1999, Talman & Keough 2001), among several others.

Australian coastal waters have not been immune to the global increase in marine NIS, despite Australia's relative geographical isolation. Australian marine and estuarine habitats are now home to more than 129 NIS and a further 209 cryptogenic species of unknown origin (Hayes et al. 2005). In Australia, most research on NIS

and associated development of management options has focused on recent arrivals that have established in the last 15-20 years (e.g. Talman & Keough 2001, Ross et al. 2002, Walton et al. 2002, Ross et al. 2003b, a, Ross et al. 2004). Extensive research has been conducted on the so-called 'high profile' species identified by their perceived or demonstrated capacity to impact marine communities. These include the northern Pacific seastar, *Asterias amurensis* (Ross et al. 2002, 2003b, a, Ross et al. 2004, Ross et al. 2006), the eastern Atlantic clam, *Corbula gibba* (Talman & Keough 2001), the European green crab, *Carcinus maenas* (Walton 2001, Walton et al. 2002), and the Japanese kelp, *Undaria pinnatifida* (Valentine & Johnson 2003, 2004, 2005), all of which highlight the potential problems posed by invasive species entering Australia's natural marine ecosystems.

Despite extensive research indicating potentially devastating impacts of NIS, it is widely recognized that resources available to combat them are limited (Ross et al. 2002, 2003b, a). Further, not all NIS necessarily have major impacts on their recipient communities. NIS must therefore be prioritized for management based on the most current and scientifically robust estimate of their imminent and potential impact to native assemblages and habitats, and so impact assessment makes an important contribution in the prioritization process (Parker et al. 1999, Byers 2002a, Ross et al. 2002, 2003b).

1.2 QUANTIFYING IMPACTS AT DIFFERENT LEVELS OF BIOLOGICAL ORGANISATION

Research on NIS has identified five levels of biological organisation at which impacts of NIS can be measured (adapted from Parker et al. 1999):

1) Effects on individuals, including measurable impacts on demographic rates such as mortality and growth, or on morphometric features and other life history characteristics.
2) Genetic effects (including hybridization).
3) Population-level effects, including changes in the abundance and distribution of populations of particular species.
4) Community-level effects, including alterations to community characteristics such as species richness, diversity and community composition.
5) Effects on ecosystem processes such as nutrient flux rates and pathways, production, respiration and community metabolism.

Most research attempts to investigate impacts of NIS at only one or two of these levels. Effects on population dynamics, such as changes in the abundance or distribution of native species, and effects on individuals, primarily on their growth and development, are the impacts most commonly investigated (Parker et al. 1999, Crooks 2002). Genetic effects, impacts on entire communities and effects on ecosystem processes are the least studied. Moreover, it is relatively rare that research attempts to address impacts across multiple levels of biological organisation (Parker et al. 1999, Crooks 2002).

The level at which ecologists elect to conduct research is often determined by economic imperatives, or the perception of potential ecological impact. Thus, research questions may relate to impacts on native species of particular interest (e.g. commercially important species), in which single species or population dynamic

approaches may be most useful. For example, NIS may be perceived to potentially impact native species via competition for food and space or directly via predation (see reviews by Byers 2009, Rilov 2009), which can be addressed directly through population level and individual level approaches. Alternatively, an impact assessment conducted at the community or ecosystem level, which measures impacts on species richness, diversity, evenness community composition and productivity or metabolic requirements may be used to provide an estimate of impact more appropriate for 'scaling-up' to larger temporal and spatial scales (Thrush et al. 1997a, Thrush et al. 1997c, Parker et al. 1999, Crooks 2002). Moreover, there is an increasing consensus that it is important to understand impacts of NIS at an ecosystem function or process level (Parker et al. 1999, Ruiz et al. 1999, Grosholz et al. 2000), and particularly across multiple trophic levels within the system (Grosholz & Ruiz 2009).

Given that measuring impacts of NIS provides useful information for setting priorities for management, integrated approaches involving multiple methods at a number of levels of biological organisation are likely to produce the most robust assessment of a NIS' impact. Additionally, the most comprehensive assessments will also address impacts across multiple spatial and temporal scales (Parker et al. 1999, Ruiz et al. 1999, Crooks 2002, Ross et al. 2003b, a). Therefore, an integrated assessment of the impact of a NIS, conducted at multiple spatial, temporal and conceptual scales, is likely to provide a robust indication of where limited management resources might most usefully be allocated (Parker et al. 1999, Ruiz et al. 1999, Crooks 2002, Ross et al. 2003a).

1.3 QUANTIFYING IMPACTS AT DIFFERENT TEMPORAL AND SPATIAL SCALES

One of the most challenging aspects of studying NIS is quantifying impacts that have accrued over long temporal scales, and to predict the potential spatial and temporal dynamics of impacts into the future. This is logistically difficult as in many cases the absence of comprehensive baseline data collected prior to the invasion of NIS preclude definitive identification of impacts, so that assigning causality to observed changes is equivocal. For species where comprehensive baseline data do exist, ecologists can potentially employ Before-After-Control-Impact (BACI) and Beyond-BACI experimental designs, which can be powerful tools for identifying impacts and can help to attribute causality (Underwood 1991, 1992, 1994). Although these experimental designs were developed to detect environmental disturbances, these kinds of designs can also be applied to quantifying impacts of NIS, provided that baseline data are well replicated (preferably across a variety of temporal and spatial scales).

Unfortunately, cases where comprehensive baseline data exist are an exception rather than the norm, particularly when attempting to identify impacts that have occurred and accumulated over an extended period of time. The question as to how ecologists quantify impacts of NIS when baseline data are scarce or completely lacking is pervasive. Some ecologists accrue information on biological, ecological and life history characteristics of the invasive species in its native range and compare these to the same characteristics of the species in the newly invaded habitat. While this may be a valuable exercise as a first assessment of potential

impacts and useful in directing the focus of impact assessment, it cannot provide a quantitative assessment of a NIS' impact.

Other studies have compared sites where the invasive species is not yet established to those where it has. Again, while this approach can be useful, interpretation is fraught given that it is rarely possible to unequivocally assign causality of observed differences. This is exemplified by Ross et al. (2006) where spatial differences in the composition of soft-sediment assemblages were correlated with both the presence of predatory seastars and differences in sediment size composition between 'control' and putative 'impact' sites, and so a clear interpretation of observed differences was not possible.

In the absence of robust data on response variables prior to the establishment of a NIS, there is little choice but to rely on a 'weight of evidence' approach, where impacts are estimated at a variety of spatial and temporal scales using a combination of survey and experimental techniques (Byers & Noonburg 2003, Ross et al. 2003b, a, Ross et al. 2004). Despite its obvious limitations, this approach has demonstrated that it is possible to identify the mechanisms of impact which can provide valuable information in assessing management options.

1.4 QUANTIFYING STRUCTURAL AND FUNCTIONAL IMPACTS OF INVASIVE SPECIES

Research into the impacts of NIS on ecosystem level processes, particularly to the flow of nutrients and energy following the arrival of a NIS, are fundamental impacts that are often overlooked, in part due to the complexities involved in assessing such

impacts. However, NIS in marine environments are capable of drastically altering the structural integrity of the benthos, as well as ecosystem processes such as system-level flows of materials, productivity and boundary layer processes such as nutrient cycling and metabolic fluxes (Jones et al. 1994, 1997, Schwindt et al. 2001, Crooks 2002). Moreover, NIS can potentially control the availability of resources through manipulation of the physical state of biotic or abiotic components of the environment (Schwindt et al. 2001, Crooks 2002).

Thus, in overview, NIS (and particularly those that 'engineer' the environment in some manner) have the potential to impact ecosystem processes via a number of mechanisms (Vitousek 1990, Crooks 2002). First, NIS may utilize resources (particularly nutrients) in a manner that alters patterns of biogeochemical cycling, which in turn affects the availability and flow of resources to native species. Second, NIS can alter food webs and therefore the transition of biomass or energy through a system. Third, the NIS may affect disturbance regimes, effectively governing the availability and quality of abiotic resources. NIS capable of impacting ecosystems through one or more of these mechanisms threaten the integrity and functionality of native ecosystems by interfering with both the biotic and abiotic resources that fundamentally characterize the ecosystems themselves (Jones et al. 1997, Crooks 2002).

Despite the potential impacts of NIS to ecosystem level processes, rarely are they quantified directly. Often impacts of NIS on the ecosystem processes of native assemblages have generally been inferred from alterations to the native habitat and

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faunal community structure (Crooks 2009 and references therein). While there is no argument that assessing changes to faunal abundance, diversity and community composition following the arrival of a NIS is both fundamental and critical in the preliminary assessment of impact, estimating effects of NIS on ecosystem level processes, in parallel with community structure, will provide a more comprehensive understanding of the overall impact.

1.5 STUDY SPECIES

The New Zealand screwshell (*Maoricolpus roseus*) is a large, solid turritellid gastropod with a broadly conical spire. The shells can be up to 87 mm in length and 25 mm in width (Powell 1979 in Bax et al. 2003). Shells range in colour from fawn to reddish or purplish brown, faintly marbled or streaked in darker brown, and the operculum is thin, horny, circular and multispiral in nature (Powell 1979 in Bax et al. 2003).

Maoricolpus roseus is abundant around most of New Zealand, often occupying the benthos at densities of several hundred individuals per square metre. The species proliferates in benthic habitats not subject to wave action, but is also known to occupy more exposed habitats, such as those in crevices on rock walls in areas like Fiordland, and in sheltered pockets on more exposed reefs (Bax et al. 2003). In New Zealand, *Maoricolpus roseus* occupies various habitats from the low-water mark to a depth of ~ 200 m, although is more commonly observed in soft sediment habitats, varying in coarseness from fine silt, to gravels (Scott 1997, Bax et al. 2003). The

greatest densities are observed on coarse substrata rather than sites dominated by high silt content (Allmon et al. 1994).

Maoricolpus roseus was first recorded in Australian waters by Greenhill in 1963, although anecdotal evidence suggests it may have been introduced from New Zealand to south-eastern Tasmanian waters in the 1920's (Scott 1997, Bax et al. 2003, Reid 2003, Gunasekera et al. 2005, Probst & Crawford 2008). The species is suspected to have been accidently introduced, either as semi-dry ballast in trade vessels or accompanying shipments of live oysters. The oyster species *Tiostrea chilensis* and/or *Crassostrea glomerata* were sporadically imported to Tasmania from the late 1800s to bolster a failing local oyster industry (Bax et al. 2003). The imported oysters were sold at local markets, and were kept fresh by being suspended in crates in the local estuary (Dartnall 1969). In the *ca.* 90 years since its arrival, *M. roseus* has become one of Australia's most widespread marine NIS, expanding northwards along Australia's east coast as far as northern New South Wales (Nicastro et al. 2009), with the majority of high-density aggregations occurring in Victoria, Bass Strait and south-eastern Tasmania (Allmon et al. 1994, Bax et al. 2003, Reid 2003, Gunasekera et al. 2005).

In Australia, *M. roseus* occupies similar habitats and exhibits similar ecological characteristics to the species in its native range of New Zealand. The species occupies a range of habitats from muddy silts to rocky reef, and regularly attains densities of 600 - 1200 m^{-2} (Allmon et al. 1994), and up to 2500 m^{-2} (Reid 2003),

although it is most common on shelly substrata and coarse sands (Bax et al. 2003, Reid 2003) over a depth range of 0 - 200 m.

Maoricolpus roseus is primarily a sedentary ciliary suspension feeder (Scott 1997, Bax et al. 2003) relying on water currents to provide a mechanism for food particle and seston delivery and waste removal. While ciliary suspension feeding is the most common feeding mode among turritellids (Scott 1997), some species such as *Gazameda gunnii* are capable of switching to alternate modes (i.e. deposit feeding), particularly in times when the abundance of pelagic sources of nutrition are limiting (Allmon 1988). There is some evidence that *M. roseus* may also be capable of switching to a deposit feeding mode, but the possibility requires further investigation (Davenport & Bax 2002).

Despite occupying the soft-sediment benthos at extreme densities, *M. roseus* exhibits rapid growth rates, particularly when conditions are favorable, but like all turritellids, growth rates and abundances have been shown to depend on environmental conditions such as the degree of exposure, phytoplankton concentration, substratum type and complexity, population density, predation and temperature (Allmon et al. 1994, Scott 1997). *Maoricolpus roseus* tends to exhibit a logarithmic growth pattern, growing faster and laying down significantly greater amounts of shell while young. The growth and development of the shell at later ages is slower, which is suspected to reflect an ontogenic decline as more energy is invested into reproduction. Growth is seasonal, with the most rapid growth during the warmest months, particularly in the first year (Scott 1997, Bax et al. 2003).

Most research on *M. roseus* has focused on identifying characteristics of reproduction and embryonic development (Gunasekera et al. 2005, Probst & Crawford 2008). In summary, *M. roseus* has separate sexes, in contrast to the native *Gazameda gunnii* which is a protandrous hermaphrodite. Reproduction occurs during the Australian summer (October-February) and fertilized eggs develop to an early stage embryo (~50 μm) through to a trochophore stage (75-150 μm length) and into a veliger (100-200μm in shell length, reaching 1.5 whorls) within the mantle cavity of the female (Bax et al. 2003). Larvae released from the female are planktonic and therefore exhibit high potential for extensive pre-settlement dispersal (Probst & Crawford 2008). Moreover, there is evidence to suggest that *M. roseus* larvae are planktotrophic (Probst and Crawford 2008), highlighting the potential for larvae to compete with native species that also possess planktotrophic larval stages.

1.6 THESIS OBJECTIVES AND OUTLINE

It can be problematic to quantify the immediate and potential threat of NIS across relevant spatial and temporal scales. Usually there are several factors which make it difficult to unambiguously attribute changes in a system to the NIS. First, there is often a paucity of robust base-line data prior to the arrival of the NIS. Second, NIS are typically well established before they are identified. Third, changes coincident with the invasion of a NIS can be confounded with other concomitant environmental impacts which makes it difficult, if not impossible, to isolate and quantify the effect of the NIS. In this thesis, I aim to overcome these issues by using a multi-method approach conducted across a variety of spatial and temporal scales and across

several levels of biological organisation in assessing the impacts of the New Zealand screwshell (*Maoricolpus roseus*) in Tasmania.

I use a combination of surveys and *in situ* manipulative experiments to separate and quantify impacts at individual, population, community and ecosystem levels of biological organization. Further, cognisant of the absence of baseline information prior to the arrival of *M. roseus*, particular experimental and survey designs are deployed, which enables quantification of impacts developed over long periods, and how these impacts may vary spatially and temporally. This can be achieved by individually quantifying impacts of the different screwshell 'states' (e.g. live shells, dead and empty shells and dead shells supporting hermit crabs), because depending on the area, screwshell accumulations may consist primarily of live individuals (95 % alive), or mostly dead screwshells, and in some benthic habitats, the dead shells are almost totally occupied by hermit crabs. For example, in eastern Bass Strait, vast areas support aggregations of screwhells at high densities (1200 m^{-2}) most of which (99%) are dead and occupied (85 %) by hermit crabs. Therefore, in areas where *M. roseus* has invaded, the benthic habitat is likely to represent a mosaic of patchily distributed accumulations of screwshells comprising of the different screwshell 'states'. As a result, separating the impacts of screwshells in different 'states' elucidated how the impact may vary across this spatial and temporal patchiness of screwshell accumulations observed in nature.

Against this background, the aims of the present work are to:

1) Determine the impact of the introduced New Zealand screwshell (*Maoricolpus roseus*) on the structure and function of native soft sediment communities.
2) Determine the impact of *M. roseus* on the distribution, growth and condition of commercially important scallop species.
3) Conduct a holistic assessment of the impact of *M. roseus* across a multitude of temporal and spatial scales, and across several levels of biological organisation.
4) Determine whether impacts warrant exploration of management measures to combat the spread of *M. roseus* and discuss the potential for several methods of managing the impact of the species.

In chapter 2, an *in situ* manipulative experiment is used to assess impacts of *M. roseus* on the structure of native soft sediment communities. Impacts were assessed at high (1500 ind. m^{-2}) and low (200 ind. m^{-2}) screwshell densities, and impacts related to the presence of live screwshells were assessed independently of impacts associated with dead screwshells, and dead screwshells containing hermit crabs. The experiment was conducted over 20 months at a single site and was devised to assess immediate impacts associated with live *M. roseus* independently of intermediate to long-term impacts associated with accumulations of dead and empty shells, and dead shells supporting hermit crabs. By considering the effects of accumulations of dead shells, whether occupied by hermit crabs or not, the approach allowed for longer-term impacts to be inferred. The major findings from this work were that the

presence of screwshells (particularly at high densities) promoted increased inhabitancy of the area by a diverse array of taxa, but primarily by epifauna, which attached to the physical substratum provided by the shells. Differences were also evident between the different screwshell states (i.e. alive vs. dead and empty vs. dead with hermit crabs), with benthos supporting live screwshells being depauperate in filter-feeding bivalves and amphipods, but rich in errant and sedentary polychaetes and predatory gastropods, when compared to communities associated with dead screwshells. Communities associated with screwshells containing hermit crabs exhibited high abundances of crustacean taxa, but a reduced presence of sedentary polychaetes.

Chapter 3 focuses on the immediate and longer term impacts of the screwshell on community metabolism. Oxygen flux (production and utilisation) was measured in the suite of treatments in the experiment described in Chapter 2. As in Chapter 2, impacts related to the presence of live screwshells were assessed independently of impacts associated with dead screwshells, and dead screwshells containing hermit crabs. This enabled a more holistic assessment of impact, relating structure and function at the community level over relatively long time scales. Moreover, as for Chapter 2, by assessing the effects of accumulations of dead shells, longer-term impacts could be inferred from the adopted approach. Evidence from this work showed that communities supporting high densities of screwshells exhibited higher oxygen flux (both production and utilisation of oxygen) when compared to benthos without screwshells. In contrast to the results of Chapter 2, the effects of the different screwshell states were far more obvious. Communities associated with

living screwshells utilised twice as much oxygen as communities associated with dead and empty shells, or shells occupied by hermit crabs. Moreover, differences in oxygen fluxes were mismatched with differences in community structure, when the results were compared to those of Chapter 2.

Chapters 4 and 5 focus on the impacts of screwshells on an important commercial species in the region, the scallop *Pecten fumatus*. In Chapter 4, impacts on the distribution of scallops at both large ($5x10^1$ m) and small (10^1 mm) scales are inferred from surveys at several spatial scales, and these data are complemented with a small scale *in situ* manipulative experiment designed to test behavioral responses of *P. fumatus* to aggregations of the screwshell. This work suggests that screwshells interfere with micro-habitat selection by scallops, effectively excluding them from otherwise soft-sediment habitat. I identify the most plausible mechanisms of impact and discuss the potential implications to the commercial and recreational scallop fisheries.

Given clear effects on the distribution and behaviour of commercial scallops (Chapter 4), in Chapter 5, I examine whether screwshells influence the growth and condition of juvenile commercial scallops (*Pecten fumatus*). The intent was to complement results observed at the population level (Chapter 4) by assessing impacts at an individual level. Documented individual level impacts of NIS include effects of competition, predation and facilitation (see reviews by Byers 2009, Rilov 2009). The approach employed a manipulative experiment to quantify the impact of *M. roseus* on the growth, condition and survivorship of *P. fumatus* juveniles. Again,

impacts associated with live and dead *M. roseus* shells were compared, and the relative effects of interspecific and intraspecific competition were quantified. The work identified a significant reduction in the growth and condition of *P. fumatus* juveniles that occupied areas of benthos with living screwshells. Further, there was an obvious negative impact of dead screwshells, although this was only evident at low scallop densities.

Each of the chapters 2-5 were devised to assess impacts of *M. roseus* at individual, population and community levels, to consider impacts on both structure and function, and at a number of temporal and spatial time scales. In the final Chapter I attempt to combine the key findings from chapters 2-5 to provide a holistic assessment of the impact of *M. roseus* in SE Tasmania. The assessment points to the need to implement measures to minimize risk of further spread of *M. roseus*, and identifies several imperatives in this endeavor.

Readers should note that chapters 2-5 are developed as stand-alone manuscripts, prepared for submission to peer-reviewed journals. Accordingly, some repetition is unavoidable, particularly in chapter introductions and in the descriptions of the sites and methodology.

CHAPTER 2

IMPACTS OF INTRODUCED NEW ZEALAND SCREWSHELLS (*MAORICOLPUS ROSEUS*) ON NATIVE SOFT SEDIMENT COMMUNITIES.

2.1. ABSTRACT

Introduced New Zealand screwshells (*Maoricolpus roseus*) form extensive accumulations in many subtidal soft-sediment habitats in SE Australia, greatly altering the complexity and habitat characteristics of the benthos. In this study I investigated impacts on community structure and habitat characteristics of *M. roseus* using an *in situ* manipulative experiment. Impacts were assessed at high (1500 ind. m^{-2}) and low (200 ind. m^{-2}) screwshell densities, and impacts related to the presence of live screwshells were assessed independently of impacts associated with dead screwshells, and dead screwshells containing hermit crabs. Soft-sediment communities associated with high densities of screwshells were very different to those inhabiting adjacent patches of bare sediment, and were characterised by a higher abundance of total macroinvertebrates and species richness. These differences were primarily attributed to a diverse epifaunal community present in screwshell treatments that were almost totally absent from control plots without screwshells. In general, bryozoans, chitons, stone corals, hermit crabs, amphipods and polychaetes were more prevalent in plots with screwshells at high densities than

in control plots irrespective of whether the shells were alive, dead and empty or containing hermit crabs.

Communities associated with live screwshells were vastly different to those in the presence of dead screwshells or screwshells containing hermit crabs at the same density. Relative to patches with accumulations of dead screwshells, communities with live screwshells at similar densities were depauperate in filter-feeding bivalves and amphipods, but supported high abundances of errant and sedentary polychaetes and predatory gastropods. In contrast, communities associated with screwshells containing hermit crabs exhibited high abundances of crustacean taxa, but a massively reduced presence of sedentary polychaetes.

Differences in community structure between treatments of different screwshell density were attributed to differences in habitat complexity (additional 3-dimensional physical heterogeneity associated with the physical presence of the screwshells) and the sediment size and stability of the benthos. Differences in faunal community composition were also interpreted with respect to sediment size structure, with high density treatments possessing higher silt content than low density treatments and controls, which then correlated with higher species diversity and abundances of dominant taxa. The organic matter content of sediments did not differ significantly among treatments and did not correlate with the composition of communities from different treatments. Impacts on community structure of live screwshells were distinctly different to those associated with dead and empty screwshells or screwshells occupied by hermit crabs. Given that *M. roseus* has

potentially occupied large areas of benthos, across a wide range of habitats for an extensive period of time, I conclude that *M. roseus* has greatly altered the community structure in these habitats, and should *M. roseus* continue to invade new areas, significant 'engineering' to both the physical structure of the benthos, and the community structure of soft-sediment assemblages will likely occur.

2.2. INTRODUCTION

The introduction and establishment of non-indigenous species (NIS) is considered a significant force of ecological change in both terrestrial and aquatic systems worldwide. Exemplified in a growing body of literature, both human-mediated introductions and range extensions of NIS have often affected the structure and function of native assemblages, particularly in marine realms (Carlton et al. 1990, Carlton & Geller 1993, Carlton 1996b, a, Cohen & Carlton 1998, Ruiz et al. 1999, Ruiz et al. 2000, Crooks 2002, Ross et al. 2002, 2003b, Ruiz & Hines 2004). Despite this, the majority of NIS arguably have little effect on the structure or function of their recipient communities (Johnson 2007). Given that resources available to develop adequate management strategies for NIS are often limited, NIS must be prioritised for management action based on their imminent and potential impacts to native assemblages and habitats (Byers 2002b, Ross et al. 2002, 2003b, a).

Research to quantify impacts of NIS in Australia has typically targeted relatively recent arrivals, particularly those that have established in the last 15-20 years (e.g. Talman & Keough 2001, Ross et al. 2002, Walton et al. 2002, Ross et al. 2003b, a). Further, those NIS gaining the most attention have been large and/or aesthetically spectacular, and abundant in habitats adjacent to marinas, wharves and boat ramps where they are visible to the general public. Most attention has been given to voracious generalist predators, species capable of impeding local commercially important species, or species deliberately introduced for aquaculture. Examples include the northern Pacific seastar, *Asterias amurensis* (Ross et al. 2002, 2003b, a,

Ross et al. 2006), the eastern Atlantic clam, *Corbula gibba* (Talman & Keough 2001), the European green crab, *Carcinus maenas* (Walton et al. 2002) and the Pacific oyster, *Crassostrea gigas* (Nugues et al. 1996). Here I investigate impacts of a long-established and wide-spread invader of soft-sediment habitat, the New Zealand screwshell, *Maoricolpus roseus* (Quoy and Gaimard 1834), which established in S.E. Australia *ca.* 90 years ago (Bax et al. 2003, Reid 2003, Gunasekera et al. 2005).

The New Zealand screwshell is a turritellid gastropod inadvertently introduced into Tasmanian waters, most likely during the 1920s (Scott 1997, Bax et al. 2003, Reid 2003, Gunasekera et al. 2005, Probst & Crawford 2008). It is believed to have either accompanied shipments of live oysters or arrived in the cobble ballast of trade ships (Bax et al. 2003). Since its arrival, *M. roseus* has become one of Australia's most widespread introduced marine species, expanding northwards along Australia's east coast as far as northern New South Wales (Nicastro et al. 2009), with the majority of high-density aggregations occurring in Victoria, Bass Strait and eastern Tasmania (Allmon et al. 1994, Gunasekera et al. 2005). In its native range of New Zealand, *M. roseus* occupies all substrata from soft-sediments to exposed rocky habitats over a depth range of 0 - 200 m. In Australia, *M. roseus* also occupies a similar range of depths and habitats from muddy silts through to rocky reef, although it is most common on shelly substrata and coarse sands (Bax et al. 2003, Reid 2003). *M. roseus* regularly attains densities of 600 - 1200 m^{-2} (Allmon et al., 1994), and at some sites up to 2500 m^{-2} (Reid 2003), with high spatial variability in the proportion of live animals ranging from mostly live to mostly dead. Furthermore, of the dead

shells, a large fraction are often occupied by hermit crabs (Reid 2003). Given that *M. roseus* has potentially occupied large areas of a variety of habitats over a long period, the potential exists for *M. roseus* to have ecological, environmental and economic ramifications that surpass those more high profile introduced species restricted to shallow inshore environments. Despite this, comprehensive research into its basic ecology and impacts on native assemblages is lacking.

Aggregations of *M. roseus* shells at high densities have the potential to greatly transform or 'engineer' (sensu Crooks 2002) the benthic habitat, increasing three-dimensional structural complexity and heterogeneity of the substratum, altering current flow and affecting rates of sedimentation and food supply, all of which are well known to affect faunal community structure (Carlton et al. 1990, Jones et al. 1994, 1997, Crooks & Khim 1999, Lenihan 1999, Parker et al. 1999, Strayer et al. 1999a). Further, the persistent nature of the shells provides a firm substratum for the attachment of filamentous algae and sessile encrusting invertebrates, while competition for food and space between screwshells and native filter feeding species, such as bivalve molluscs and native gastropods, may realise a decline in growth and abundances of native taxa (Bax et al. 2003). There is already anecdotal evidence that the native screwshell, *Gazameda gunnii* (Reeve, L.A. 1849), has ostensibly disappeared from soft-sediment habitat in areas dominated by *M. roseus*, and now exhibits a reduced distribution at low densities (Bax et al. 2003, Gunasekera et al. 2005).

Not all aggregations consist of healthy living screwshells, and accumulations of dead screwshells, which can persist for an extensive period given the massiveness of the shell, are likely to impose different kinds of impacts to native assemblages than the impacts of live *M. roseus*. For example, it has been established that accumulations of dead and empty screwshells support large populations of a native hermit crab species, *Paguristes tuberculatus* (Reid 2003). This species, now capable of occupying vast areas previously unavailable to it, is likely to have its own impact on infaunal community structure mediated by the availability of dead and empty *M. roseus* shells. Therefore, *M. roseus* has considerable potential to alter the structure of soft-sediment assemblages, both through the presence of live shells and through the presence of dead and empty shells, or shells containing hermit crabs.

In this paper, I quantify the impact of *M. roseus* on soft-sediment assemblages through 20-month manipulative experiment carried out in south-eastern Tasmania. I separate the impacts of live screwshells from impacts of dead and empty shells and of dead shells containing hermit crabs, and I link differences in community structure to the alteration of habitat characteristics by the screwshell, in particular, to changes in sediment size and organic matter. Both direct and indirect impacts and the potential spatial and temporal variability of these impacts are discussed.

2.3. METHODS

2.3.1 STUDY SITE

The study site is a shallow sheltered embayment in south east Tasmania, Australia (Bligh Point, D' Entrecasteaux Channel, Fig. 2.1). Bligh Point exhibits a shallow rocky reef that descends abruptly to sandy soft-sediments at ~ 6 m. The site also supports sparsely populated patches of sea grass (*Zostera sp.*) and sporadic beds of sponges. The deeper region of the site (12 m) is soft-bottom habitat dominated by a variety of fine and coarse sands in addition to accumulations of shell grit. Bligh Point displays similar sediment, depth, light and water current characteristics to that of other near-by embayments presently dominated by *M. roseus*, but the site only supports sparsely scattered, low-density patches of the screwshell. The impact of *M. roseus* at Bligh Pt. Has likely been minimal, and therefore the site was appropriate for deploying *in situ* experiments to quantify the impact of *M. roseus* on the native soft-sediment community structure and habitat characteristics.

2.3.2 EXPERIMENTAL PROTOCOL

Treatments in the experiment included 3 levels of screwshell 'state' (live screwshells, dead and empty screw shells, and dead screwshells with 50% occupancy by hermit crabs) crossed with 2 levels of screwshell density (200 m^{-2} and 1500 m^{-2}). Experimental plots were 0.75 m x 0.75 m, delineated by a 100 mm high polyvinyl chloride (PVC) frame to maintain the initial densities of screwshells and hermit crabs whilst minimizing interference to current regimes at the sediment-water interface. Pilot studies indicated that the PVC frame sufficiently maintained the densities of shells as initially deployed. In addition to the treatments in the main

experiment, two 'control' treatments were also used, comprising of PVC frames over unmanipulated areas without screwshells, and unmanipulated areas without either PVC frames or screwshells. There were 4 replicates of each treatment, with treatments allocated randomly and positioned 1 m apart on the seafloor. Treatment plots were arranged in a 4 x 8 grid at 12 m depth, and treatments were assigned using random number generation. The PVC frames were buried to a depth of 40 mm, leaving 60 mm exposed above the sediment to 'fence in' the screwshells.

Maoricolpus roseus were collected at nearby Dennes Point (Fig. 2.1) in 12 m depth using a dredge with an opening of 630 x 350 mm and a depth of 320 mm towed at an average speed of 1 km/hr for a period of 5 mins on 12 December 2004. Animals were then held in laboratory aquaria until they were deployed into randomly allocated experimental plots at the study site on 14 December 2004. The size distribution of shells was representative of the collection area and had a mean of 47 ± 6 mm. Live *M. roseus* were separated from dead and empty shells and shells containing hermit crabs by identifying the clear presence of an operculum inside the shell aperture. Dead and empty *M. roseus* were obtained from Blackman's Bay beach (43' 00.085 S, 147' 19.577 E). Densities inside the experimental plots were assessed monthly and maintained by adding small numbers of screwshells to respective treatment plots as needed. Addition of screwshells was required on only one occasion (14 January 2006).

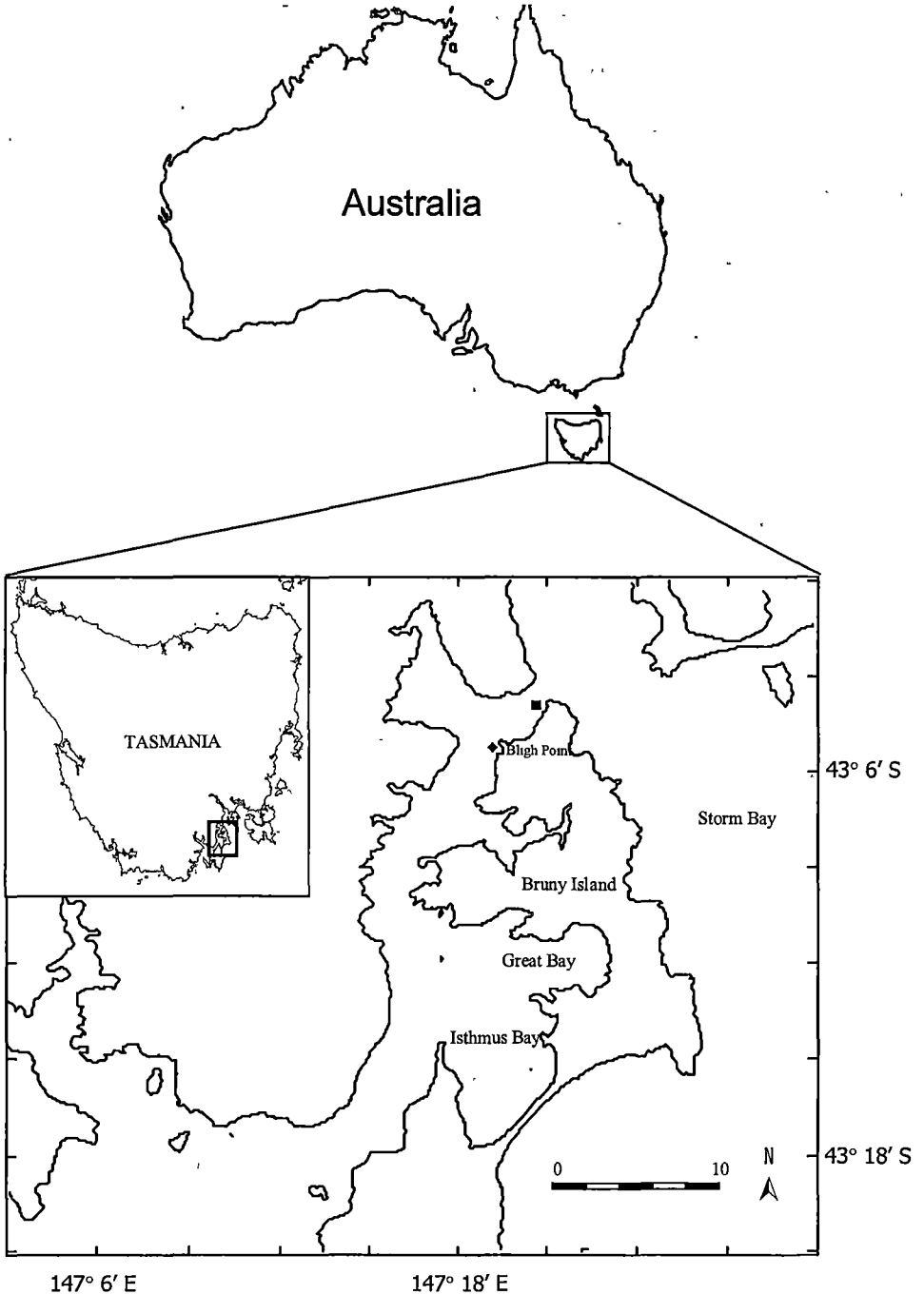

Figure 2.1. Map of the D'Entrecasteaux Channel, showing the location of the experimental study site at Bligh Point (◆) and the screwshell collection site at Dennes Point (■).

2.3.3 COLLECTION AND PROCESSING OF BIOTA AND SEDIMENT

The experiment was maintained for 20 months, concluding on 10 October 2006, after which the experiment was sampled destructively. To avoid the possibility of edge effects associated with the presence of the PVC frames, a 0.5 x 0.5 m quadrat was used to delineate the inner most 0.25 m^{-2} area of each plot, within which the collection of all biota and sediment samples was performed. Six sediment cores, 80 mm deep and 30 mm diameter were extracted from each experimental plot and used to estimate sediment size structure and organic matter content. Cores for sediment size analysis were stored at -4 °C and sediment fractionation accomplished by wet sieving cores through a ∅ sieve series of 4 mm, 2 mm, 1 mm, 500 μm, 250 μm, 125 μm and 63 μm, and drying the relative fractions to constant weight at 105 °C for 24 hrs. Cores for organic matter content were stored at -80 °C before being dried initially at 105 °C for 24 hrs, and organic matter content was calculated by a loss on ignition (LOI) procedure, which involved incinerating at 550 °C for 4 hrs (Heiri et al. 2001).

Once cores were removed, all screwshells (and associated epifauna) were carefully collected by divers from each treatment plot, fixed in buffered 5 % formaldehyde solution, and stored for identification of epifauna. Following removal of shells, each plot was suction - sampled to a depth of 100 mm with an air lift and the contents of each experimental plot retained in separate 1 mm mesh bags. Suction samples were fixed in a buffered 5 % formaldehyde solution with Rose Bengal stain. In the laboratory, epifauna attached to screwshells were counted and removed to 70 %

alcohol. Samples were sieved over 4 mm, 2 mm and 1 mm mesh sizes. All infauna were removed from the 4 mm portion, however, to cope with the volume of the 2 mm and 1 mm aliquots, they were split using a Jones-Style riffle splitter into quarters, and two of the sub samples analyzed. All sorted infauna were removed to 70 % alcohol, counted and identified to family (for polychaetes, amphipods, isopods, tanaids and decapods) or species level (for bryozoans, chitons, stone corals, gastropods and bivalves).

2.3.4 STATISTICAL ANALYSIS

2.3.4.1 Comparison of fauna across treatments

To assess and depict differences between treatments in community structure, I used non-metric multi-dimensional scaling (nMDS) and permutational multivariate analysis of variance (PERMANOVA). Analyses were based on Bray-Curtis dissimilarities derived after a square-root transformation of the data. The nMDS ordinations were developed using PRIMER 5 software (Clarke and Gorley 2001), while PERMANOVA routines were as described in Anderson (2001) and McArdle & Anderson (2001).

Analyses of community structure were carried out on different components of the fauna. First, an nMDS ordination was carried out including all taxa identified to the lowest taxonomic level. This analysis considered both the infauna and epifauna, including encrusting invertebrates attached to screwshells. Because this analysis included fauna directly associated with (and often attached to) the screwshells themselves, but there was no analogous hard substratum in the control plots without

screwshells, a second nMDS was based on infauna only. A third nMDS ordination assessed differences in epifauna composition across treatments of different screwshell densities and states, which can be considered as different quantities and qualities of hard substrata. The significance of patterns observed in the nMDS plots was determined using PERMANOVA (Anderson 2001, McArdle & Anderson 2001).

Since it was of interest to identify whether *M. roseus* had any effects at a particular functional resolution (e.g. filter-feeding molluscs), a final analysis considered differences in the relative abundance of particular functional groups, which were broadly based on feeding mode and mobility. While these groups were not strictly 'functional groups' *per se*, they were taxonomic groups categorized broadly based on their function. Therefore, for ease of clarification, such groups are hereafter referred to as 'functional groups'. After pooling taxa into these groups, patterns were depicted based on principle components analysis (PCA) ordination (with associated biplot) and the significance of differences among treatment groups determined by parametric multivariate analysis of variance (MANOVA). This enabled identification of those functional groups most important in explaining differences in community structure across the experimental treatments. PCAs were carried out using PRIMER 5 (Clarke and Gorley 2001), and MANOVAs performed using SAS 9.1 statistical package (Statistical Analysis System).

Univariate model I ANOVA was used to compare mean species richness, total abundances and diversity (Shannon-Wiener) and abundances of select taxonomic

groups and species among treatments. ANOVAs were also performed using the SAS 9.1 statistical package.

All PERMANOVA (conducted on total community structure), MANOVA (conducted on functional groups) and univariate ANOVA models (conducted on selected taxa) had the same basic design. They included the fixed effects of 'screwshell density' (2 levels: high/low), crossed with 'screwshell state' (3 levels: live screwshells, dead screwshells and dead screwshells with 50% occupied by hermit crabs) and the 'screwshell density * screwshell state' interaction. In the event that the main analysis yielded a significant interaction, an *a-posteriori* Ryan-Einot-Gabriel-Welsch (REGWQ) multiple range test was conducted to determine the nature of the interaction. The MANOVA assumptions of multinormality of residuals, homogeneity of variances among groups and homogeneity of covariances were all assessed before proceeding with the analysis. Determination of significance in MANOVA was achieved using Pillai-Bartlett Trace (V), as it is considered the most robust (Johnson & Field 1993). For ANOVAs, data and residuals were checked for normality and homoscedasticity, and transformed as necessary to stabilise variances on the basis of the relationship between group standard deviations and means (Draper & Smith 1981).

Following overall tests for treatment effects in the MANOVAs and ANOVAs, two orthogonal *a priori* planned comparisons were also conducted. First, the fenced control (C+F) was compared with all plots containing screwshells at high densities (H). In the second, the fenced control was compared with all plots containing low

densities of screwshells (L). Since these contrasts were completely orthogonal, no adjustment to the type I error rate (α) was required. These comparisons were conducted as it enabled comparisons of bare sediment (controls) to that of areas occupied by screwshells (irrespective of state) at both low and high densities.

2.3.4.2 Comparison of sediment structure across treatments

Sediment size structure was analysed using a PCA/biplot ordination followed by MANOVA. This enabled identification of particular sediment size fractions contributing to the differences in sediment structure between experimental treatments. The design of the MANOVA was identical to that described above (i.e. included terms for 'screwshell density', 'screwshell state' and the 'density*state' interaction). The same orthogonal planned contrasts used in the analysis of functional groups were also performed on the sediment size data (C+F vs. H and C+F vs. L). Univariate ANOVAs were then conducted for selected sediment sizes, identified as those fractions with the highest weightings in the PCA/biplot analysis. Data were assessed for normality and homoscedasticity, and transformations made as necessary to ensure validation of the assumptions of both the MANOVA and ANOVA models.

2.3.4.3 Linking patterns in community structure to sediment structure

Correlation of patterns in community structure with patterns in sediment size involved the use of the BIOENV procedure within the PRIMER 5 software package (Clarke & Gorley 2001). The biological data consisted of communities identified to the highest taxonomic resolution from individual treatment plots and the analysis

was based on Bray-Curtis dissimilarity determined from square-root transformed data. The sediment size data were untransformed, and relationships between samples based on a normalized Euclidian distance similarity measure. The Spearman rank correlation method was used in the BIOENV procedure.

2.3.4.4 Assessment of caging effects

To test for the possibility of caging artifacts arising from the use of the PVC frames, a series of analyses were devised to compare community structure between fenced (C+F) and unfenced controls (C-F) in the absence of screwshells. In the case of total community structure, a 1-way PERMANOVA was performed including a single fixed effect of 'fence' (present/absent). When data were pooled into function groups (as above), MANOVA was used to compare functional groups between fenced and unfenced controls, again with a single fixed effect of 'fence' (present/absent). The same design was implemented in 1-way univariate ANOVAs used to test the impact of the PVC frame on species richness, total abundances, diversity (Shannon-Wiener) and abundances of selected functional groups and species that were particularly abundant. Lack of significant differences between C+F and C-F plots would indicate negligible effects of the PVC frames, enabling ready interpretation of treatment effects in the main experiment.

2.4. RESULTS

2.4.1 TOTAL FAUNAL COMPOSITION

A total of 20, 930 individuals were recorded in the study, and significant differences were observed in the total numbers of individuals between the different treatments. Generally, the high density treatments exhibited higher total abundances of individuals than the low density treatments and controls (Fig 2.2a, Table 2.1). On average, high densities of screwshells supported 792 ± 55 individuals/0.25 m^{-2}, low density plots 578 ± 28 individuals/0.25 m^{-2} and the control (fenced) 559 ± 11 individuals/0.25 m^{-2}. This was however, dependent on screwshell 'state' with high densities of live screwshells yielding higher total abundances than the other screwshell 'states' at the same density (Fig 2.2a, Table 2.1). The low density treatments were not significantly different to the controls in terms of total macroinvertebrate abundance.

A total of 178 taxa were recorded in the study, including 54 mollusc, 62 crustacean, 9 echinoderm, 35 polychaete and 17 epibiont taxa (e.g. bryozoans, stone corals, and chitons). As for the total abundance of individuals, species richness was also notably higher in plots containing high densities of screwshells, although this was not dependent on screwshell 'state' (Fig 2.2b, Table 2.1). On average, high densities of screwshells supported 60 ± 3 taxa/0.25 m^{-2}, low density plots 51 ± 3 taxa/0.25 m^{-2} and the control (fenced) 56 ± 1 taxa/0.25 m^{-2}.

Of the 178 individual taxa, 62 were never recorded in control plots (mostly from crustacean, mollusc and epibiont families), compared with 11 taxa (predominately

bivalve molluscs) that occurred in control plots that were never observed in plots containing screwshells. Treatments with low densities of screwshells supported fewer species than the fenced control, although the difference was not significant. No significant differences in Shannon Wiener diversity (H') were detected across any of the treatments or controls (Fig 2.2c, Table 2.1).

2.4.1.1 *Impacts of screwshell density*

Treatment plots of differing screwshell density had vastly different community structures. The nMDS conducted on the complete faunal communities showed three clear groupings, corresponding to differences in screwshell density (Fig 2.3a). Separation of communities from control plots and low density treatments containing screwshells were more distinct in the nMDS conducted on epifauna alone (Fig 2.3c),

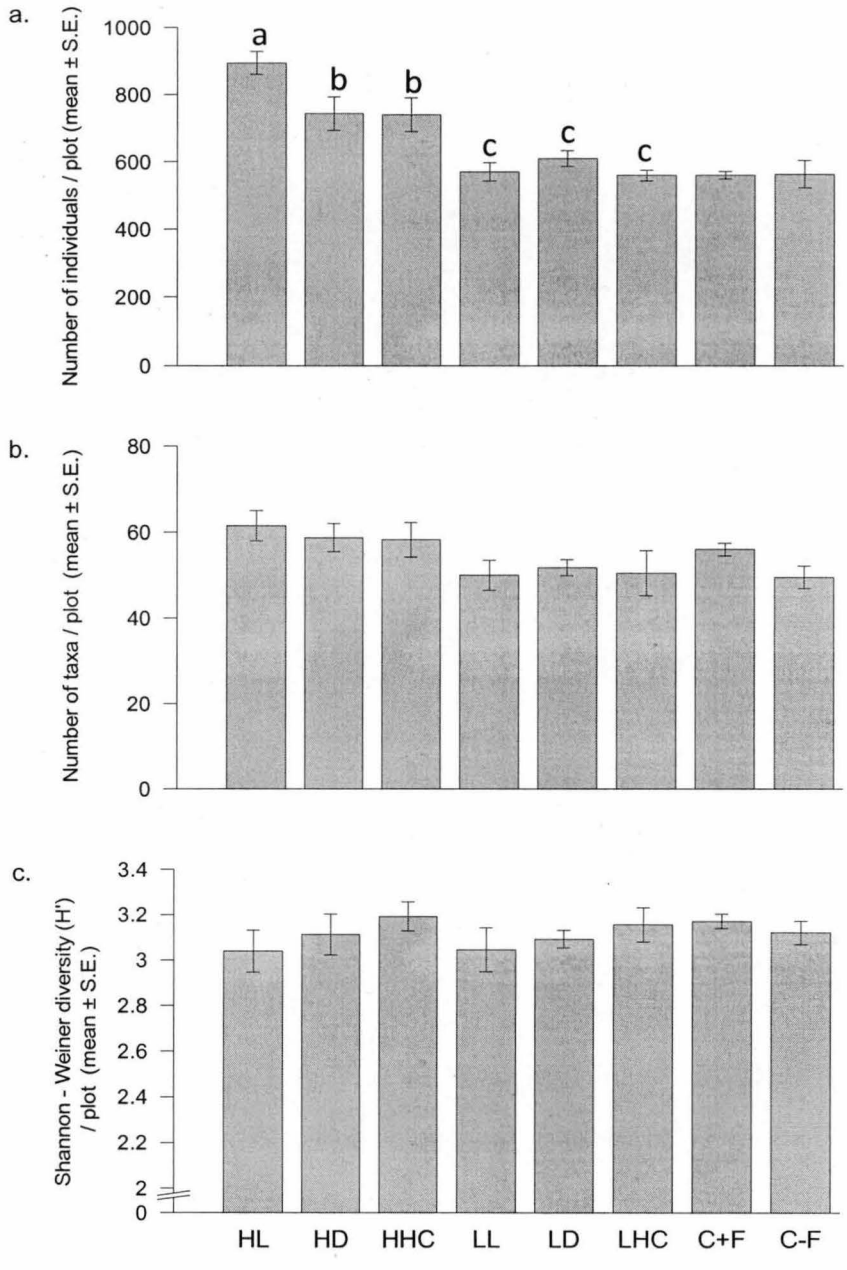

Figure 2.2. Faunal responses to treatments with screwshells. (a) total abundance of individuals, (b) total taxa, (c) Shannon-weiner diversity (H') across treatments. All values are means ± S.E. from n=4 replicate plots of each treatment. HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control. For main analyses where significant density*state interactions were detected, the REGWQ groups are positioned above the respective treatments. In the REGWQ groups, analogous letters denote the same groupings. The control groups were assessed in separate *a priori* comparisons and are therefore not included in the REGWQ groups.

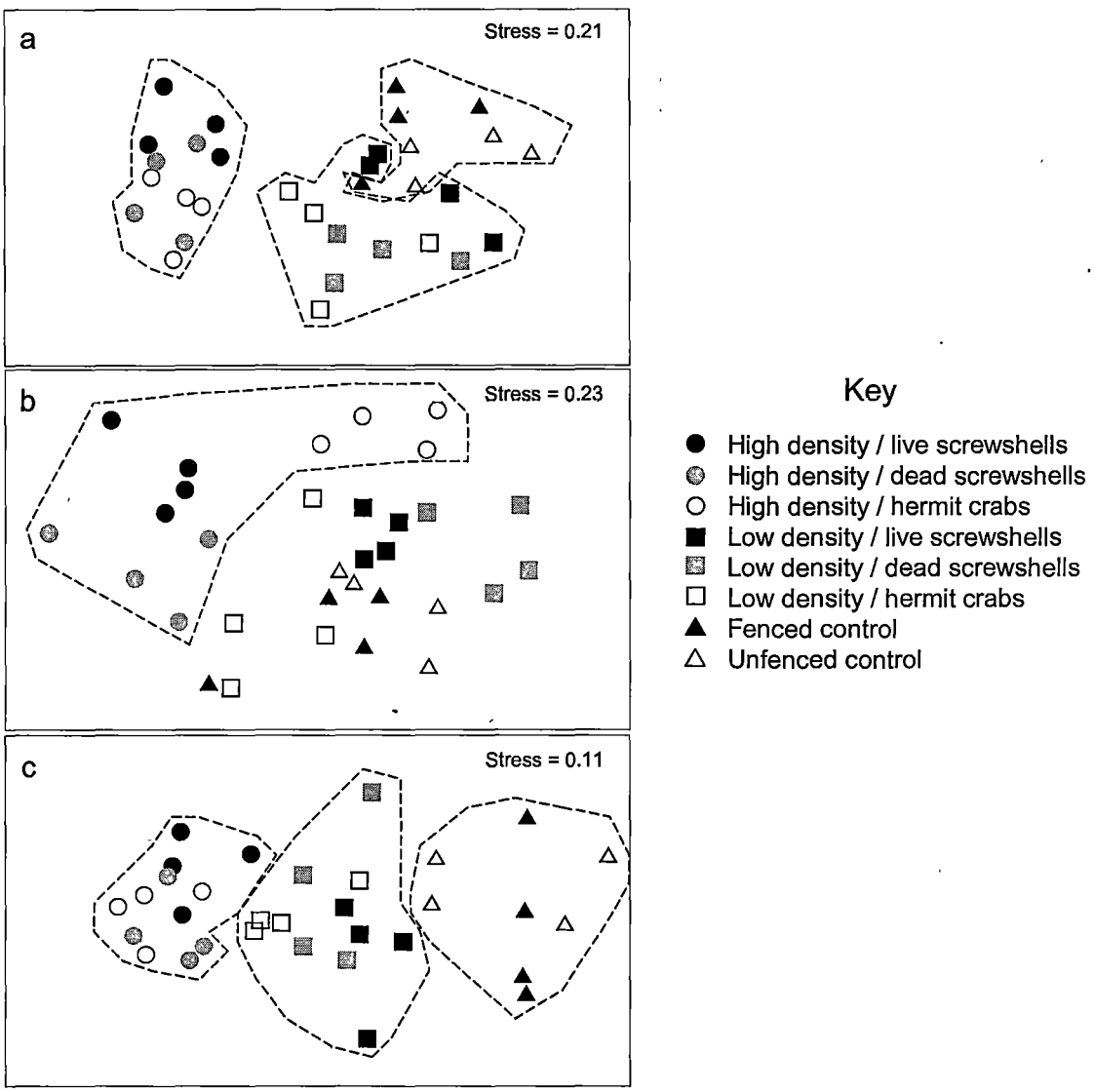

Figure 2.3. nMDS ordinations showing separation of the different communities across all treatments. (a) entire community identified to highest resolution, (b) infauna only (omitting epifauna), and (c) epifauna only. For the analysis of the complete community, significant differences were detected among different screwshell densities and states (PERMANOVA, screwshell state: MS= 1541.59, $F_{2,18}$=3.07, P=0.0002; screwshell density: MS= 1236.17, $F_{1,18}$=2.46, P=0.008; state*density: MS= 900.98, $F_{2,18}$=1.79, P=0.019). Analogous results were also obtained for infauna only (PERMANOVA, screwshell state: MS= 1226.91, $F_{2,18}$=2.15, P=0.0001; screwshell density: MS= 1152.4, $F_{1,18}$=2.03, P=0.0159; state*density: MS= 946.7443, $F_{2,18}$=1.67, P=0.0249) and epifauna only (PERMANOVA, screwshell state: MS= 3625.83, $F_{2,18}$=17.5, P=0.0001; screwshell density: MS= 1566.75, $F_{1,18}$=7.56, P=0.0017; state*density: MS= 531.14, $F_{2,18}$=2.56, P=0.0479). Dotted lines indicate separation of groups based on density.

Table 2.1. Results of fixed effects ANOVA comparing among screwshell treatments mean total abundances, species richness, Shannon-Wiener diversity and abundance of functional groups and common taxa. Results are of overall ANOVAs comparing among treatments of different screwshell states and densities (Main Analysis), and include the planned comparisons C+F vs. H (which compares fenced controls to all treatments with high densities of screwshells) and C+F vs. L (which compares fenced controls to all treatments with low densities of screwshells. The planned comparison to test for effects of the PVC fence is also included (C+F vs. C-F). Significant P values are shown in bold face (P<= 0.05).

	Main analysis				Planned comparisons					
					Density				Fence	
		P values			CF vs. H		CF vs. L		CF vs. CNF	
Variable	MS_{resid}	State	Density	State*Density	MS_{resid}	P value	MS_{resid}	P value	MS_{resid}	P value
Degrees of freedom	18	2	1	2	12	1	12	1	6	1
Total number of individuals	5128.7	0 089	**<0.001**	**0.041**	6262 9	**<0.001**	1670.62	0.410	5320.6	0.936
Species richness	55.1	0.932	**0.010**	0.812	41.5	0.366	45.48	0.202	17.8	0.072
Species diversity (H')	0.1	0.269	0.802	0.964	0.1	0.518	0 02	0.358	0.1	0.436
Total molluscs	129.9	0.480	0.103	0.704	65.2	0.499	62.79	0.480	132.8	0.683
Predatory gastropods	78.5	0.430	0.667	0.437	0.2	0.156	45.72	**0.033**	17.8	0.183
Nassarius nigellus	42.9	0.218	**0.031**	**0.039**	21 9	0.833	53.88	0.133	19.6	0.939
Grazing gastropods	461.5	**0.006**	0 582	0.516	285.8	0.157	481.87	0.147	936.9	0.339
Bittium granarium	29.9	0.433	0.688	0.613	31.1	0.345	26.45	0.447	41.6	1.000
Pisinna varicfera	219.3	**<0.001**	0.849	0.383	207.6	**0.023**	235.81	**0.025**	564.4	0.144
Bivalves	324.1	**0.010**	0.096	0.829	404 3	0.109	250.79	0 448	296.2	0.586
Timoclea cardioides	85.2	0.690	0.119	0.490	92.4	0.179	80.27	0.741	132.8	0.683
Ostrea angasi	110.9	**0.031**	**0.014**	0.261	135.7	**0.022**	30.66	0.085	41.6	1.000
Total crustaceans	1153.4	0.666	0.067	0 056	859.4	**0.019**	905.56	0.294	449.9	0.226
Crabs	16.1	0.576	0.057	0.546	18.2	0.300	6.70	0.664	4.3	0.426
Hermit crabs (*Pagurixus handrecki*)	303.2	0.851	0.316	0.278	0.2	**0.003**	299.27	0.098	60.9	0.099
Decapod shrimps	13.4	0.139	0.043	0.162	12.0	0 130	12.29	1.000	45.9	0.655
Alpheis richardsonii	3.9	0.818	**0.006**	0.968	4.6	**0.036**	2.73	0.670	2 00	0.477

Table 1.0 Cont.

	Main analysis				Planned comparisons					
					Density				Fence	
		P values			CF vs. H		CF vs. L		CF vs. CNF	
Variable	MS_{resid}	State	Density	State*Density	MS_{resid}	P value	MS_{resid}	P value	MS_{resid}	P value
Degrees of freedom	18	2	1	2	12	1	12	1	6	1
Isopods	14.6	0.514	0.108	0.303	34.2	0.942	26.5	0.346	56.3	0.719
Tanaids	330.3	0.986	0.482	0.176	451.2	0.905	151.6	0.600	255.5	0.689
Kalliapseudes sp.	6.2	0.774	0.936	0.882	4.7	0.306	6.4	0.351	16.5	0.301
Apseudes sp.	11.5	0.829	0.319	**0.024**	63.6	0.348	55.0	0.150	52 1	0.437
Amphipods	122.2	**0.020**	**0.003**	0.234	142.3	**0.028**	149.7	0.844	249.9	0.289
Elasmopus sp.	48.8	**0.006**	**0.013**	0.180	1.3	**0.018**	45.5	0.365	22.3	0.775
Total polychaetes	1316.0	**<0.001**	**<0.001**	**0.005**	1804.6	**0.009**	276.7	0.299	427.9	0.649
Errant polychaetes	223.9	**0.012**	**0.000**	0.199	339	**0.033**	78.9	0.824	200.8	0.619
Nereidae A	32.7	**0.023**	**0.046**	0.301	37.4	0.094	24.1	0.626	33.8	0.771
Sedentary polchaetes	524.3	**<0.001**	**<0.001**	**0.001**	685	**0.006**	120.3	0.170	228.8	0.875
Lumbrineridae A	45.0	**<0.001**	**<0.001**	**<0.001**	50.5	**<0.001**	85.7	0.141	66.0	0.318
Amphinomidae A	32.5	**<0.001**	**<0.001**	**<0.001**	36.5	**<0.001**	0.0	0.619	40.3	**0.034**
Total bryozoans	143.9	0.324	**<0.001**	0.446	203.7	**<0.001**	12.4	**<0.001**	1.6	0.304
Membranipora membranacea	113.6	0.485	**<0.001**	0.430	162.2	**<0.001**	8.3	**<0.001**	0.3	0.207
Triphyllozoon moniliferum	3.4	0.316	**0.002**	0.470	4.3	**0.018**	0.9	0.317	0.3	0.537
Total stone corals	300.5	0.102	**<0.001**	0.146	64.1	**<0.001**	54.7	**<0.001**	109.6	0.308
Culicia sp.	267.4	0.076	**<0.001**	0.126	348.5	**<0.001**	54.7	**<0.001**	104.0	0.354
Total chitons	5.0	0.842	**<0.001**	0.355	4.9	0.067	4.8	0.171	2.3	0.056
Total echinoderms	12.4	0.779	0.218	0.938	16.9	0.706	8.1	0.587	6.6	0.217

but less distinct in the nMDS conducted on infauna only (Fig 2.3b). This suggests that the separation of the communities into distinct groups on the basis of screwshell density is related to the abundance of epifaunal taxa. Further, the PCAs and associated biplots (conducted on data organized into functional groups) also indicated that common epifaunal taxa, particularly stone corals and bryozoans, were important in the separation of treatment plots with different screwshell densities, especially between high density screwshell treatments and the controls (Fig 2.4, Table 2.2). The most prevalent of the bryozoans, *Membranipora membranacea*, was actually ~ 50 times more abundant in high density treatments than in controls. A second species of bryozoan, *Triphyllozoon moniliferum*, along with the stone coral, *Culicia sp.*, were also both ~ 5 times more abundant in high density treatments than in controls (Fig 2.8, Table 2.1). Chitons were another epifaunal taxon important in contributing to the separation of communities on the basis of screwshell density. Chitons were almost twice as common in high density screwshell treatments as in controls and ~ 4 times more abundant than in low density screwshell treatments (Fig 2.8, Table 2.1)

Although less distinct in the nMDS, infauna communities associated with high densities of screwshells nonetheless separated clearly from other treatments (Fig 2.3b). The PCAs and biplots (conducted at a broad functional group level) indicated that crustaceans, sedentary polychaetes and errant polychaetes were all more prevalent in communities associated with high densities of screwshells, than in control plots and plots with low densities of screwshells (Fig 2.4b, Table 2.2). Specifically, the hermit crab, *Pagurixus handrecki*, the amphipod, *Elasmopus sp.*, as

well as the sedentary polychaete families Lumbrineridae and Amphinomidae and the errant polychaete family Neriedae, were all more abundant in plots with high densities of screwshells than in control plots and plots with low densities of screwshell (Figs 2.6, 2.7, Table 2.2). The pistol shrimp, *Alpheis richardsonii*, was the only crustacean taxa to exhibit lower abundances in treatments with high densities of screwshells than in the controls and treatments with low screwshell densities (Fig 2.6).

Molluscan taxa were also abundant across all of the treatments and, unlike crustaceans, polychaetes and the epifauna; several molluscs were more abundant in fenced control plots than treatment plots with screwshells (Fig 2.5). Although these differences were not all statistically significant, low densities of screwshells were associated with more predatory gastropods, while grazing gastropods, particularly *Pisinna varicfera,* were slightly more common in plots supporting high densities of screwshells (Fig 2.5). Bivalves (filter feeders) were more abundant in control plots, particularly *Timoclea cardioides*, which was twice the density in control plots and in treatment plots with low screwshell densities than in treatments with high densities of screwshells (Fig 2.5). Alternatively, *Ostrea angasi*, the native oyster, was completely absent from control plots and was only observed in the presence of screwshells. This was not surprising, given that *Ostrea angasi* is an epifaunal species that requires a hard substratum for attachment, a habitat feature clearly absent from control plots.

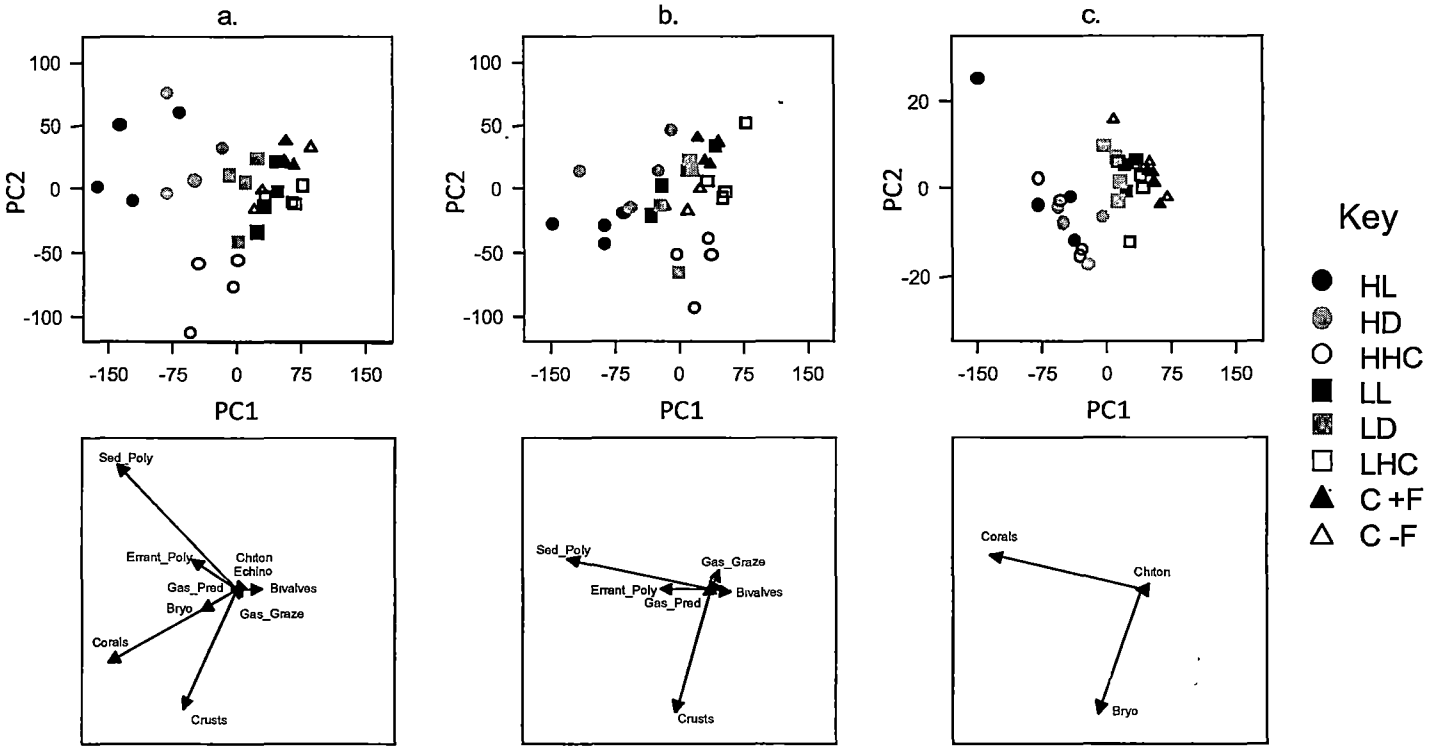

Figure 2.4. PCA ordinations and associated biplots showing the separation of communities in different treatments. All ordinations were based on data pooled into functional groups (n=4 plots per treatment). For the whole community (a) the first two principle components accounted for 72.7% (PC1=53.4%, PC2=19.3%) of the total variation; For infaunal taxa only (b) the first two principle components accounted for 75.0% (PC1=51.2%, PC2=23.9%); and for epifauna only (c) the first two principle components accounted for 98.5% (PC1=95.5%, PC2=3.0%) of the total variation. The biplots identify the groups most important in shaping the patterns observed in the PCA ordinations. Functional groups include stone corals (Corals), bryozoans (Bryo), crustaceans (Crusts), sedentary polychaetes (Sed_Poly), errant polychaetes (Errant_Poly), predatory gastropods (Gas_Pred), grazing gastropods (Gas_Graze), bivalves (Bivalves), echinoderms (Echino) and chitons (Chiton). Denotations are as indicated in Fig 2.2.

Table 2.2. Analysis of effects of screwshell treatments on functional groups. Results are of overall MANOVAs comparing among treatments of different screwshell states and densities, and the planned comparisons. C+F vs. H (fenced control compared to all high density treatments) and C+F vs. L (fenced control compared to all low density treatments) test for the effects of screwshell density with regards to the controls (no screwshells) and C+F vs. C-F test for potential caging effects. Significant P values are shown in bold face (P<= 0.05 for both main analysis and planned comparisons).

Source	df (numerator/denominator)	F	P
Total groups			
State	20, 20	8.02	**<0.001**
Density	10, 9	46.99	**<0.001**
State*density	20, 20	3.32	**<0.001**
C+F vs. H	10, 3	559.26	**<0.001**
C+F vs. L	10, 3	12.61	**0.030**
C+F vs. C-F	3, 4	1.17	0.430
Infaunal groups only			
State	14, 26	10.19	**<0.001**
Density	7, 12	7.00	**<0.001**
State*density	14, 26	2.26	**0.030**
C+F vs. H	7, 6	2.57	0.130
C+F vs. L	7, 6	0.78	0.630
C+F vs. C-F	3, 4	1.17	0.430
Epifaunal groups only			
State	6, 34	0.37	0.890
Density	3, 16	50.72	**<0.001**
State*density	6, 34	0.94	0.480
C+F vs. H	3, 10	55.32	**<0.001**
C+F vs. L	3, 10	22.55	**<0.001**
C+F vs. C-F	3, 4	0.80	0.550

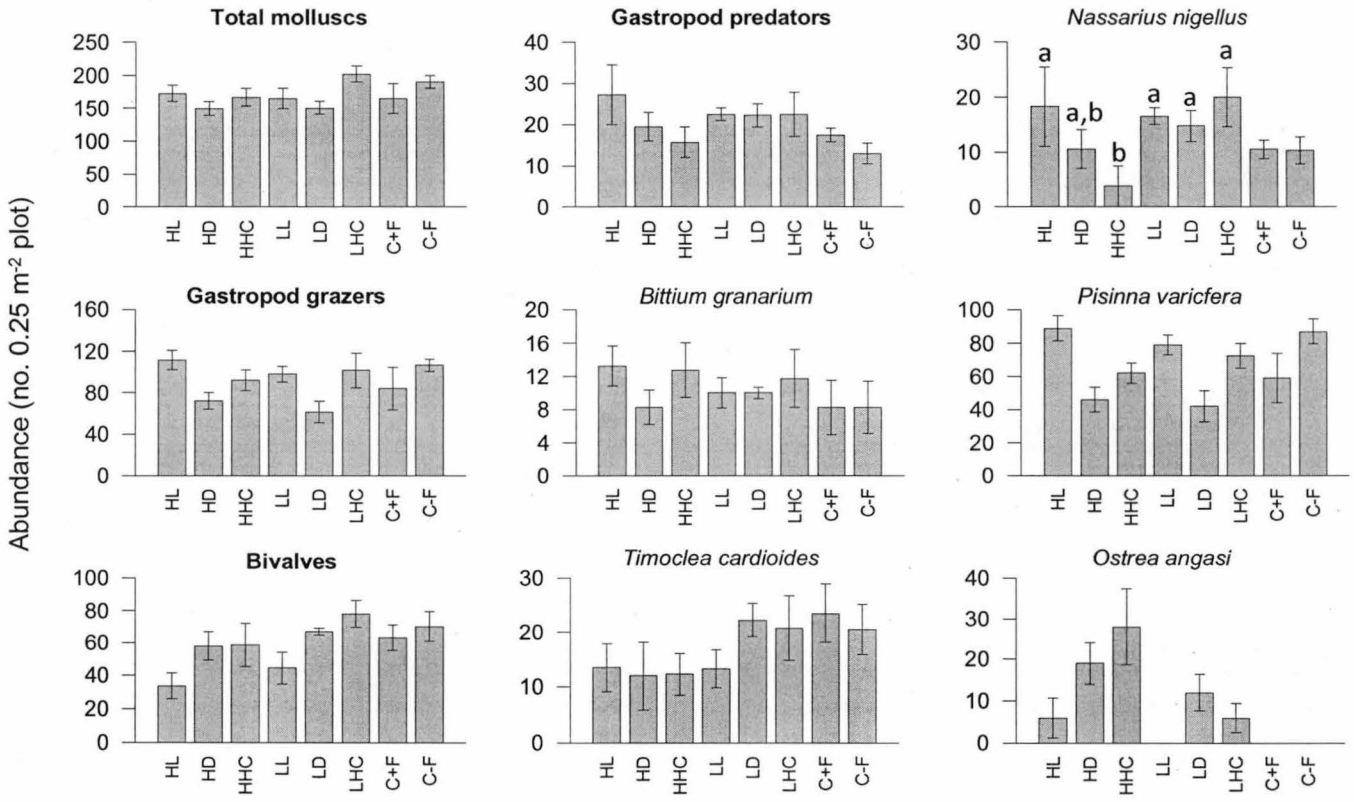

Figure 2.5. Abundance of total molluscs, mollusc functional groups and common mollusc taxa across treatments. All estimates are averages of n=4 replicate 0.25 m^{-2} plots (± S.E.). HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control. For main analyses where significant density*state interactions were detected, the REGWQ groups are positioned above the respective treatments. In the REGWQ groups, analogous letters denote the same groupings. The control groups were assessed in separate *a priori* comparisons and are therefore not included in the REGWQ groups.

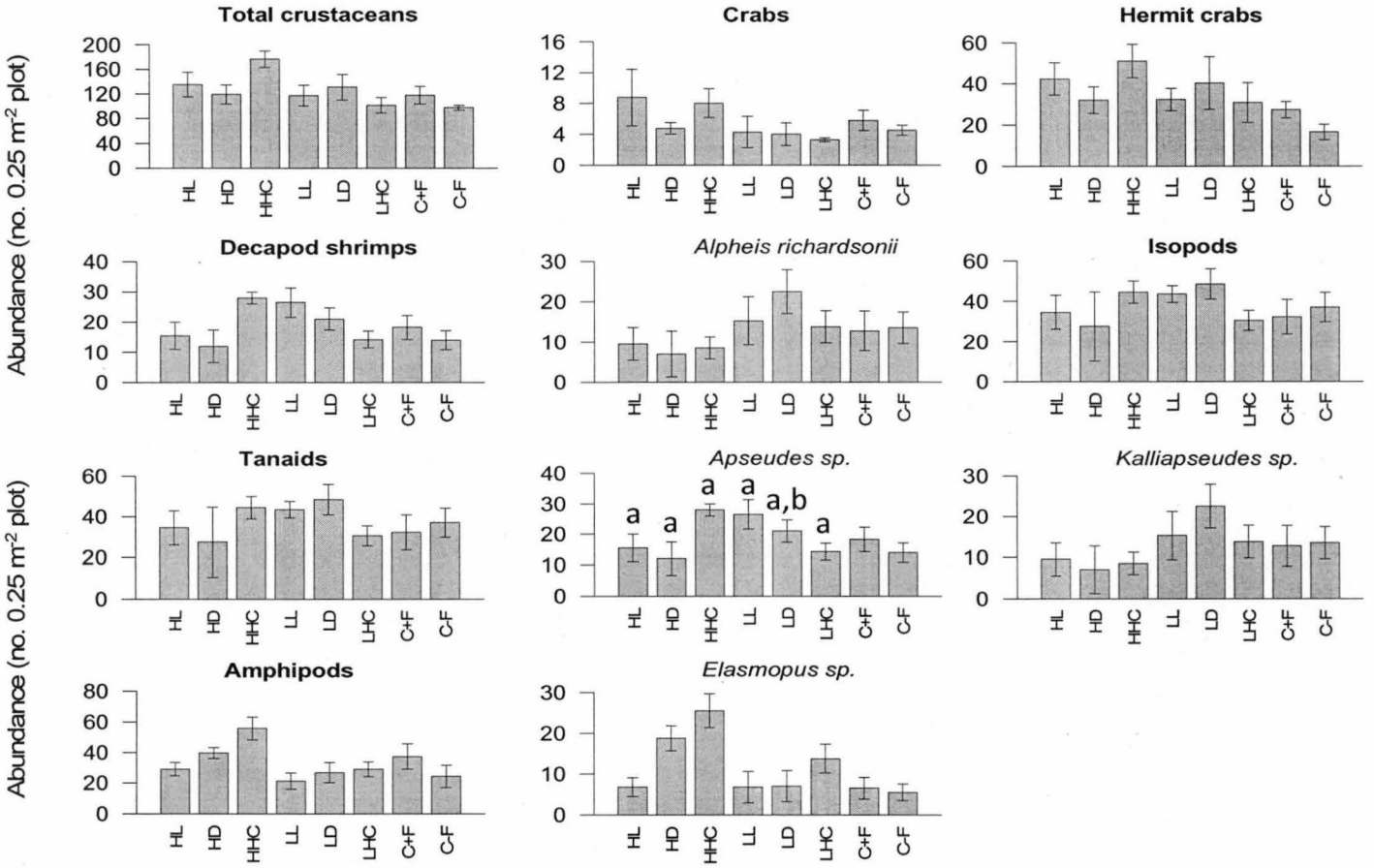

Figure 2.6. Abundance of total crustaceans, crustacean functional groups and common crustacean taxa across treatments. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control. REGWQ groups are as for Fig 2.5.

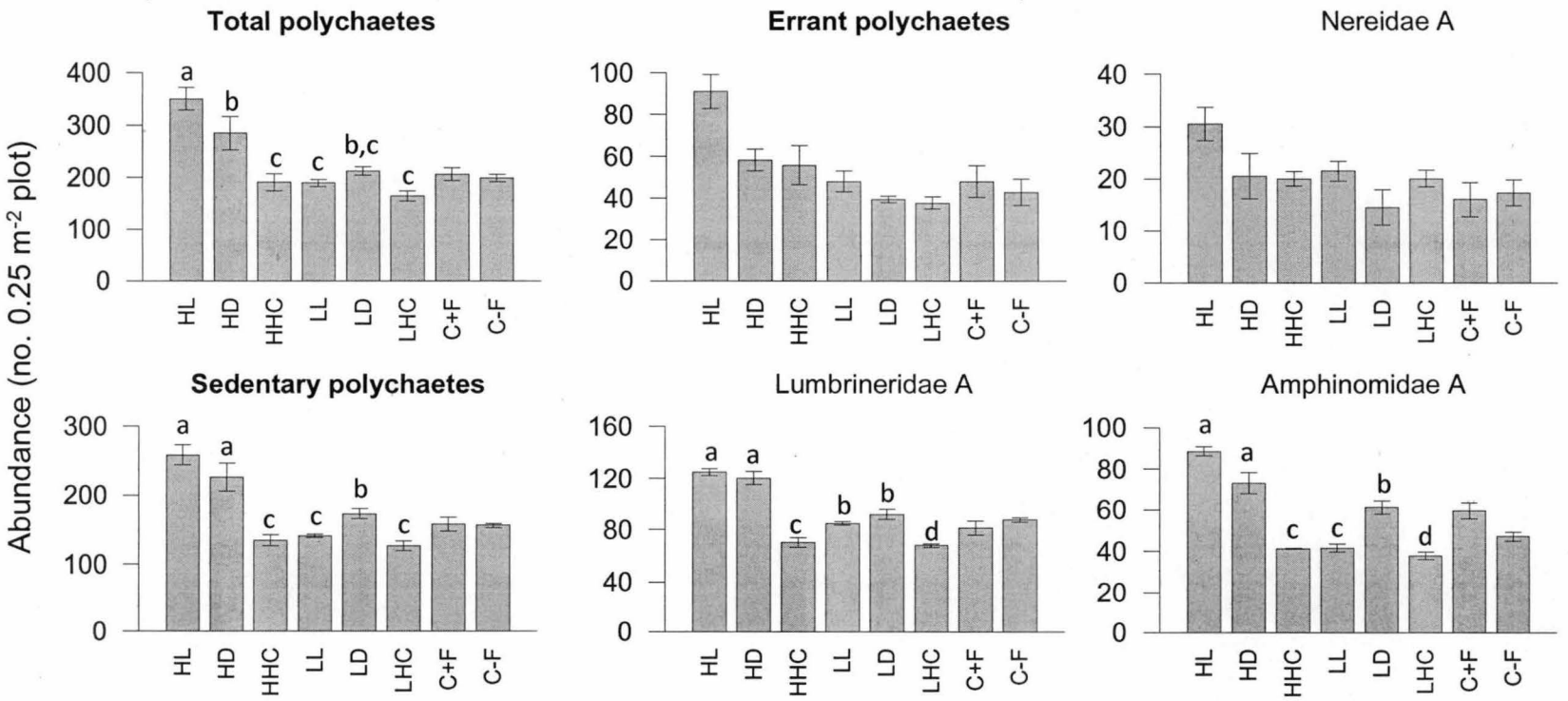

Figure 2.7. Abundance of total polychaetes, polychaete function groups and common polychaete taxa across treatments. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control. REGWQ groups are as for Fig 2.5.

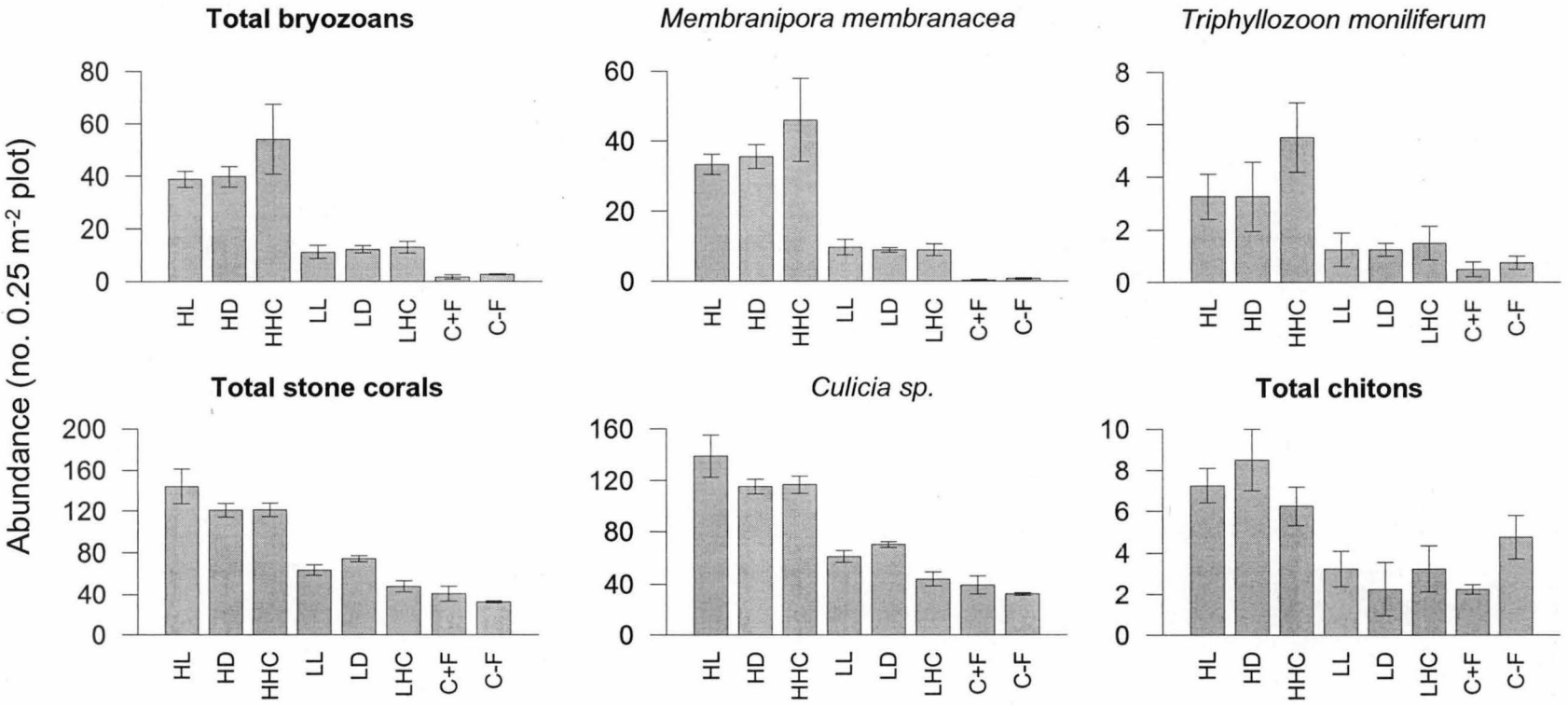

Figure 2.8. Abundance of common epifaunal species and functional groups across all treatments. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control.

2.4.1.2. Impacts of screwshell state

While screwshell density led to the most distinct differences in community structure, screwshell state also led to differences in community structure (at the same density). The nMDS ordinations conducted on the total community, epifauna only and infauna only, all revealed that communities inhabited by live screwshells were distinctly different to those with dead screwshells or dead screwshells with hermit crabs at the same density (Fig 2.3).

The abundances of epifaunal taxa (e.g. stone corals, bryozoans, chitons), which were so important in defining disparities between treatments of different screwshell densities, did not differ significantly between treatments of different screwshell states. Taxa most responsible for differences between the different screwshell states were molluscs, polychaetes and amphipods (Fig 2.4, Table 2.2). Filter feeding bivalves were far less abundant in treatments with live screwshells, while gastropod grazers, particularly *Pisinna varicfera*, were significantly less prevalent among dead screwshells (Fig 2.5, Table 2.1). Predatory gastropods were marginally more common in treatment plots containing live screwshells, although this pattern was dependent upon screwshell density (Fig 2.5, Table 2.1). Errant polychaetes were generally more abundant in plots supporting live screwshells, while sedentary polychaetes were prevalent in treatments with both live and dead and empty screwshells, but not in treatments in which screwshells were inhabited by hermit crabs (Fig 2.7). These patterns were, however, not always consistent at low screwshell densities, but were most evident at high screwshell densities (Table 2.1).

Amphipods were the only crustacean group to exhibit a change in abundance with screwshell state. Total amphipods were more abundant in the presence of both dead screwshells and dead screwshells containing hermit crabs than in treatments with live screwshells (Fig 2.6, Table 2.1). However, this pattern was clearly more evident at high screwshell densities. Conversely, decapod shrimps, crabs, tanaids and isopods showed no consistent relationship across the different screwshell states (Fig 2.6, Table 2.1). Of the remaining taxa, neither echinoderms, chitons, stone corals nor bryozoans displayed significant changes in abundance across treatments of different screwshell state at the same density (Figs 2.8, 2.9, Table 2.1).

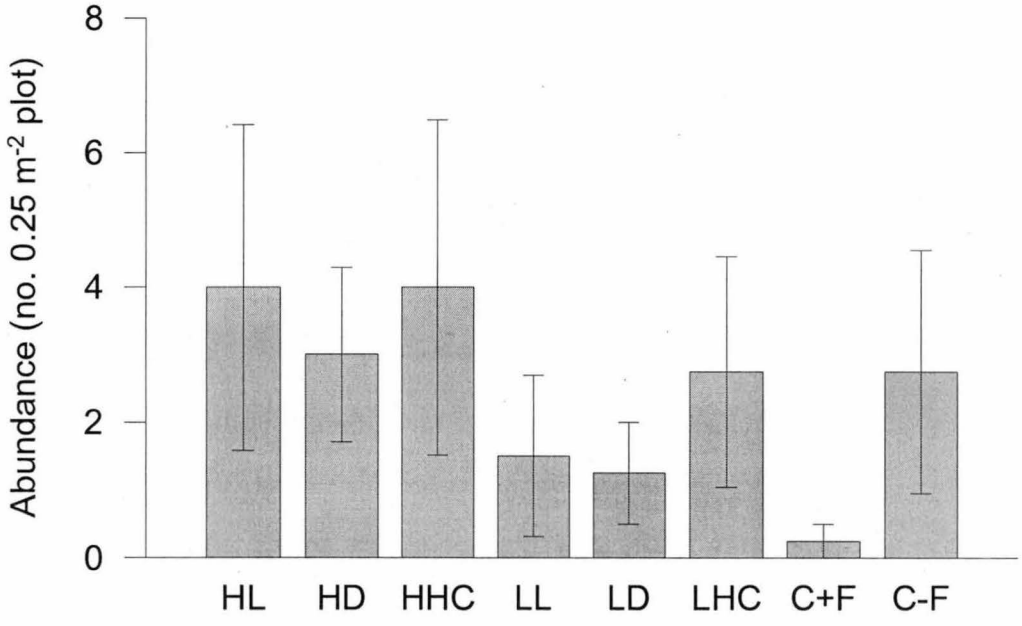

Figure 2.9. Abundance of echinoderms across all treatments. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control.

2.4.2 IMPACTS ON SEDIMENT SIZE STRUCTURE AND ORGANIC MATTER CONTENT

Sediment size structure depended strongly on screwshell density. The PCA/biplot analysis indicated a tendency for high density screwshell treatments to exhibit finer sediments, particularly evident in the 125 μm and 63 μm and <63 μm fractions (Fig 2.10). Conversely, plots without screwshells or with screwshells at low densities contained higher relative quantities of coarser sediment, particularly the 4 mm, 2 mm, 1 mm and 500 μm fractions (Fig 2.10). On average, sediment smaller than 125 μm in diameter constituted 30-35 % of a given core in treatments with high densities of screwshells, 25-30% in plots with low densities of screwshells and 20-25% in the control plots (Fig 2.11). There were no obvious differences in sediment size structure across treatments when comparing screwshell state, apart from a slightly higher quantity of finer sediments in the live screwshell treatment at high densities. Variation in organic matter content across treatments, represented as percentage of mass depleted after LOI, was also not significant (Fig 2.11).

High densities of screwshells were associated with the highest proportions of finer sediments, and a markedly different community structure than occurred in control plots and treatment plots supporting low densities of screwshells. A BIOENV analysis revealed that the best correlations between the relative sediment size fractions and the variation in community structure involved the 500 μm, 250 μm, 63 μm and the <63 μm (pan) sediment size fractions (correlation = 0.283). The smallest size fractions of 63 μm and <63 μm were present in all of the strongest correlations from the BIOENV analysis, although the best correlations were relatively weak (top 5 correlations = 0.260 – 0.283). Organic matter content was relatively uniform

across treatments, and not surprisingly, it was not identified in the strongest correlations from the BIOENV analysis.

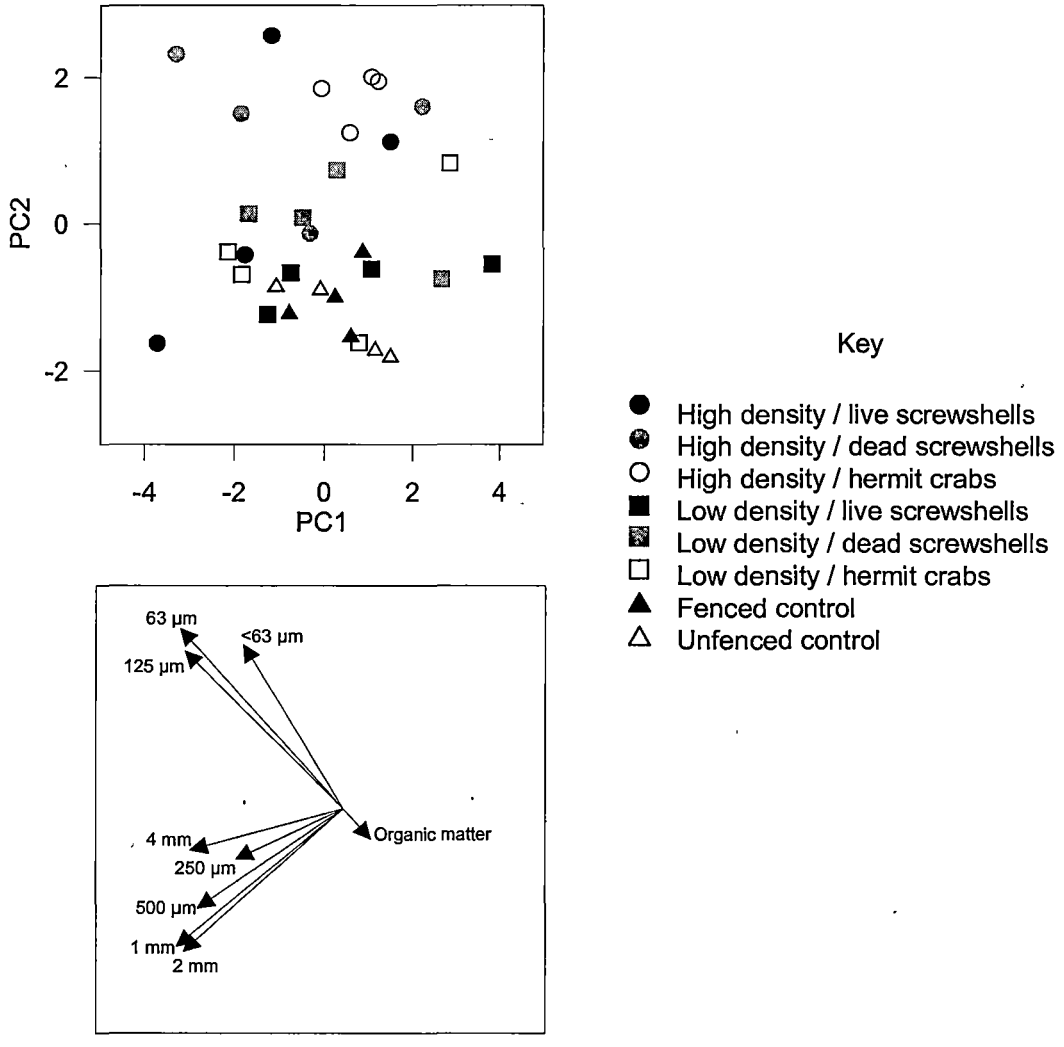

Figure 2.10. PCA ordination and associated biplot showing the separation of treatments on the basis of sediment size structure and organic matter content. The first two principle components accounted for 68.7% of the total variation observed. The biplots identify the sediment size fractions most important in shaping the patterns observed in the PCA ordination. The different treatments differed significantly in their sediment size composition (2-way MANOVA: screwshell state: $F_{12,28}$=1.41, P=0.2210; screwshell density: $F_{6,13}$=8.10, P=0.0009; state*density: $F_{12,28}$=0.96, P=0.5037) and for planned comparisons (MANOVA: C+F vs. H: $F_{6,7}$=14.58, P=0.0012; C+F vs. L: $F_{6,7}$=2.25, P=0.1560; C+F vs. C-F: $F_{6,1}$=5.22, P=0.3230).

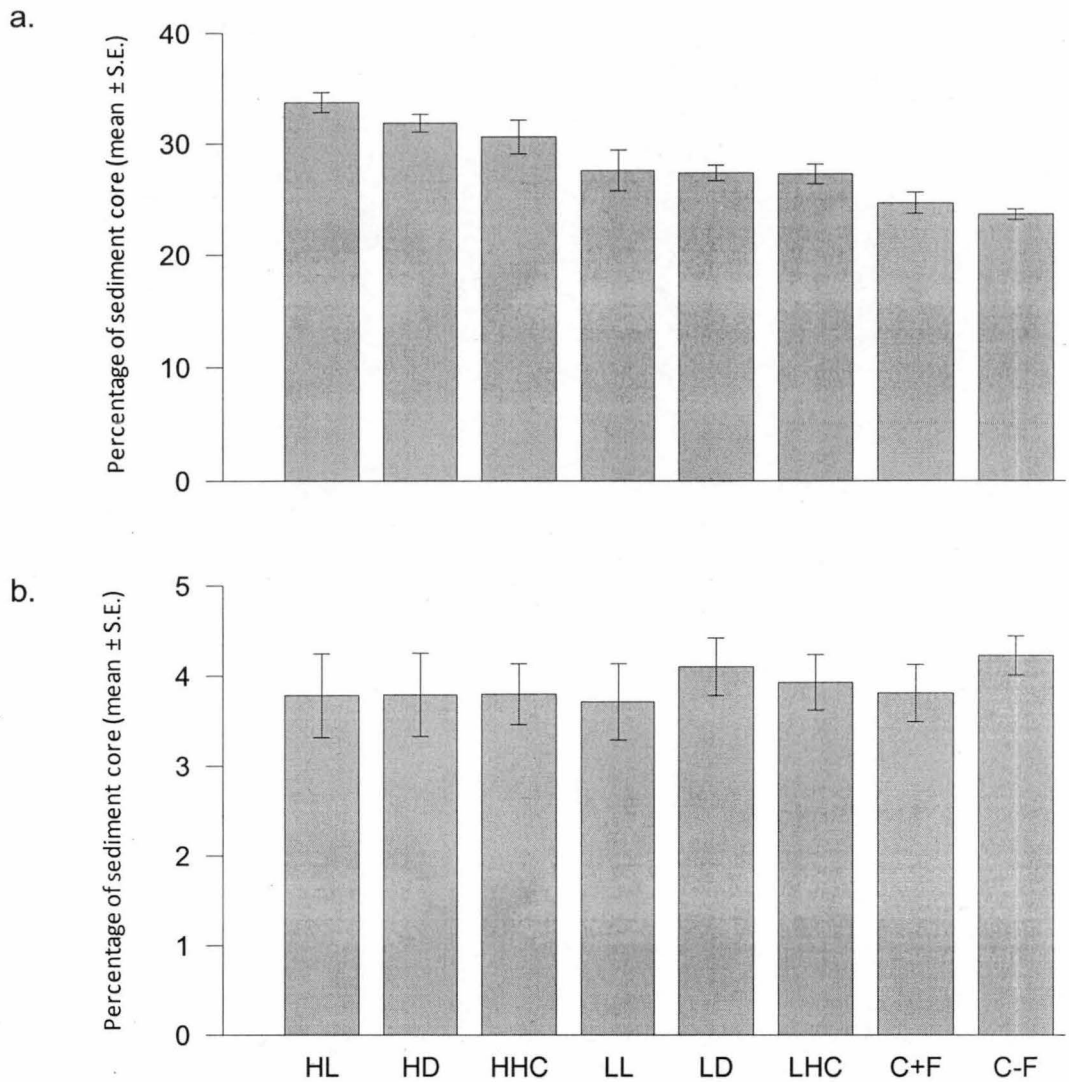

Figure 2.11. Percentage of sediment cores for each treatment comprised of (a) grain size <125 μm in size and (b) organic matter. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). High density treatments had significantly higher quantities of fine sediment < 125 μm (2-way ANOVA: screwshell state: $F_{2,18}$=0.79, P=0.4677; screwshell density: $F_{1,18}$=13.89, P=0.0015; state*density: $F_{2,18}$=0.32, P=0.7286) and for planned comparisons (ANOVA: C+F vs. H: $F_{1,12}$=17.54, P=0.0013; C+F vs. L: $F_{1,12}$=0.23, P=0.6373; C+F vs. C-F: $F_{1,7}$=2.54, P=0.3059). Organic matter content was not significantly different among treatments (2-way ANOVA: screwshell state: $F_{2,18}$=0.13, P=0. 8791; screwshell density: $F_{1,18}$=0.15, P=0.7050; state*density: $F_{2,18}$=0.12, P=0.8902) and for planned comparisons (ANOVA: C+F vs. H: $F_{1,12}$=0.69, P=0.4221; C+F vs. L: $F_{1,12}$=0.97, P=0.3447; C+F vs. C-F: $F_{1,7}$=2.10, P=0.3166). HL: high density/live screwshells, HD: high density/dead screwshells, HHC: high density/hermit crabs, LL: low density/live screwshells, LD: low density/dead screwshells, LHC: low density/hermit crabs, C+F: fenced control, C-F: unfenced control.

2.4.3 CAGING EFFECTS

The potential of artifacts that may arise from using the PVC 'fence' to maintain densities of screwshells throughout the experiment were assessed by comparing fenced and unfenced controls. Importantly, there was no difference between fenced and unfenced controls in the total abundance of fauna, total number of species or in Shannon-Weiner diversity (H') (Fig 2.2, Table 2.1). Further, evidence from the nMDS ordinations of the entire faunal community (Fig 2.3a), infauna only (Fig 2.3b) and the epifauna only (Fig 2.3c), and the PCA/biplot analysis conducted on the function groups (Fig 2.4), also indicated minimal impacts from the presence of the fence (Table 2.2). Assessment of the major functional groups, and most common taxa individually, also indicated that the presence of the PVC fence was negligible. The only taxon whose abundance differed between fenced and unfenced controls was a single species of sedentary polychaete, which was marginally more abundant in fenced than in unfenced control plots (Table 2.1). Sediment size structure did not differ across the two controls (Fig 2.10). Similarly, there was no evidence that the presence of the PVC fence either promoted settlement of finer sediments or affected organic matter content (Fig. 2.11).

2.5. DISCUSSION

2.5.1 IMPACTS OF SCREWSHELLS ON BIOTA

Despite increased global recognition of the ecological importance of some invasive species, the majority of research on marine NIS in Australia has focused on recent (within 10-20 years) arrivals perceived to pose a significant threat to their recipient environments, and where there may be some chance of controlling the species. Relatively little attention has been given to the effects of long established and wide-spread introduced species. Further, extensive research into impacts of introduced species has typically focussed solely on quantifying immediate impacts of living individuals or impacts over short temporal scales. However, quantifying impacts of NIS that have developed over extensive time periods, particularly longer than the life-span of living individuals, is also important for prioritising NIS for management responses. By deploying screwshells in different 'states' (live shells, dead shells and dead shells supporting hermit crabs) and at different densities, I was able to essentially quantify those impacts of *M. roseus* likely to occur beyond the life-span of living shells and identify the potential for these impacts to vary spatially and temporally. Critically, this is the first study I am aware of that allows for the prediction of potential impacts of a NIS beyond the life-span of living individuals.

2.5.1.1 Impacts of screwshell density

The invasion of *M. roseus* in Tasmania has drastically altered soft-sediment habitats. Particularly at very high densities of *M. roseus* (e.g. >2000 m^{-2}), the benthic substratum has effectively been 'engineered' to have greatly increased three-dimensional complexity, while there are also associated differences in accumulated

sediments of different size fractions, in the provision of hard substrata and in the extent of consolidation of the sediment. These observations suggest it is likely that boundary current characteristics at the sediment-water interface are altered by the presence of screwshells at high densities. In effect, the presence of *M. roseus* in high densities provides a unique habitat that is profoundly different to the more homogenous, low complexity soft-sediment benthos which presumably prevailed prior to its arrival. Given such extensive alteration to habitat complexity, sedimentation patterns and (arguably) boundary current characteristics, it is not surprising that I observed large shifts in species abundance, community composition and sediment size structure, as witnessed in this experiment.

High densities of screwshells had a higher density of other fauna than control plots, and were more species rich than treatments with screwshells at low densities (Fig 2.2). An increase in abundance of macro-invertebrates and species richness following invasion by a NIS is not an uncommon response (e.g. Castel et al. 1989, Posey et al. 1993, Crooks 1998b, Crooks & Khim 1999, Haynes et al. 1999, Horvath et al. 1999, Hedge & Kriwoken 2000, Wonham et al. 2005), particularly if the presence of the exotic species drastically alters, or 'engineers', the recipient environment (Crooks 2002, Wonham et al. 2005). Mechanisms that may explain the increase in species abundance and richness associated with the arrival of a NIS include increased 3-dimensional structural heterogeneity (Castel et al. 1989, Stewart & Haynes 1994, Crooks 1998b, Horvath et al. 1999); alteration to sediment size composition and stability (Vitousek 1990, Lenihan 1999, Crooks 2002, Wonham et al. 2005); changes to currents, water flows and organic matter deposition (Crooks &

Khim 1999, Wonham et al. 2005); and interference with biogeochemical cycling, oxygen concentration and nutrient fluxes (Vitousek 1990, Crooks & Khim 1999, Parker et al. 1999); any or all of which might explain the patterns observed in our experiment.

In contrast to the results of this work, some studies have revealed a decline in both total abundances and species richness in patches occupied by a newly established species in soft-sediment habitats. In particular, this was the consensus of a number of studies investigating the impact of the Pacific oyster, *Crassostrea gigas*, in which oyster-dominated areas supported fewer species and lower abundances than adjacent bare patches of soft-sediment (Castel et al. 1989, Nugues et al. 1996, Crooks 2002). They attributed this to the formation of a specialized community by the oyster, dominated by species with wide tolerances to particular conditions (e.g. hypoxia), induced following its establishment (Castel et al. 1989, Crooks 2002).

Overall community structure was notably different in treatments with high densities of screwshells than in other treatments (Fig 2.3). This differentiation is largely the result of establishment of an epifaunal community on the hard substratum provided by *M. roseus* shells (Figs 2.3, 2.4). Stone corals, bryozoans, chitons and oysters were all highly abundant in treatments of high screwshell density (Fig 2.8), and either scarce or absent in control plots. Settlement, metamorphosis and attachment of many invertebrate taxa requires the presence of a firm, consolidated substratum, pre – conditioned with a certain level of bacterial film or other fouling (see reviews by Burke 1983, Morse 1990, Rodriguez et al. 1993). The high abundance of

epifauna suggest that semi-consolidated high density aggregations of screwshells resemble a system more analogous to a low aspect, cobble reef than a soft-sediment habitat, effectively offering a highly stable substratum appropriate for promoting settlement and attachment of an extensive epifaunal community.

The increased surface area of stable substratum presented by screwshell aggregations also promoted attachment of filamentous algae and colonies of benthic diatoms (Chapter 3). In part, this high abundance of potential food may also explain the higher abundance of grazing gastropods observed occupying habitat with high densities of screwshells. The positive relationship between grazing gastropods and algal abundance has been extensively documented (see reviews by Lubchenco & Gaines 1981, Gaines & Lubchenco 1982, Wonham et al. 2005), and ready availability of filamentous algae and benthic diatoms is likely to promote a higher abundance of grazers. Higher biomass of primary producers could also explain the presence of other species more usually associated with temperate rocky reefs, including juvenile native sea urchins (*Heliocidaris erythrogramma*), which were observed in plots containing screwshells but not in control plots.

2.5.1.2 Impacts of screwshell state

Although screwshell density was clearly important in defining faunal community structure, screwshell state also appeared to influence community structure. The impacts associated with dead screwshells and screwshells occupied by hermit crabs were distinctly different to those associated with live screwshells at the same density.

The most obvious differences involved infaunal bivalves, which were substantially less abundant in treatments with live screwshells than in all other treatments (Fig 2.5). Given that all of the infaunal bivalves encountered are exclusively filter feeders, their lower abundances in association with live screwshells are most likely a result of direct competition with *M. roseus* (also a filter feeder) for food resources. Even modest densities of filter feeders are capable of greatly depleting the available pool of seston, and a reduction in quality and quantity of both benthic and pelagic phytoplankton within the benthic boundary layer by suspension feeding species has been demonstrated (Wildish & Kristmanson 1984, Frechette & Bourget 1985, Wildish et al. 1992, Jensen 1993, Josefson 1998), with effects at scales as large as entire estuaries (Nichols et al. 1990, Strayer et al. 1999a). Given that *M. roseus* accumulations can potentially reach densities of >2000 m^{-2} with up to 95% of individuals being alive, it is to be expected that this would considerably reduce the available seston, and precipitate a heightened degree of competition between *M. roseus* and other native filter feeding bivalves.

Treatments with live screwshells also exhibited higher abundances of predatory gastropods, namely *Nassarius nigellus,* and errant polychaetes, including predatory nereids. Reasons for an enhanced presence of predators in accumulations of live screwshell are unclear, and unexpected. There was little evidence that predatory whelks like *N. nigellus* preyed on *M. roseus*. Of the 1700 live screwshells recovered at the completion of the experiment, very few exhibited the characteristic bore holes as evidence of whelk predation, and often bore holes penetrated only part way through the thick *M. roseus* shells. Further, 98% of *M. roseus* shells deployed alive

at the beginning of the experiment were retrieved alive at the experiment's completion 20 months later, so if whelk predation on *M. roseus* was occurring, it wasn't significantly impacting overall densities. Increased prey in the form of *M. roseus* also doesn't explain higher abundances of predatory nereids and other errant polychaetes. The most likely explanation for increased abundances of predatory gastropods and errant polychaetes among high densities of live screwshells is related to the increase in abundance of other infaunal species, which may be viable prey for these organisms (Crooks 2002).

An unexpected result was a decrease in abundance of sedentary polychaetes associated with treatments containing hermit crabs (Fig 2.7). The reasons for this response are unclear. The hermit crab, *Paguristes tuberculatus*, is both a filter-feeder and opportunistic scavenger (Reid 2003). However, given that sedentary polychaetes, and in particular filter-feeding families such as the sabellids and serpulids, were well represented in treatments of live screwshells where the level of filter feeding is presumably very high, it is unlikely that the filter-feeding associated with the hermit crabs could account for the lower abundances of sedentary polychaetes observed in hermit crab treatments.

The most likely mechanisms by which hermit crabs exclude sedentary polychaetes are through bioturbation or other destabilization of the sediment, both of which have been important in defining benthic community structure (Hall 1994, Jones et al. 1997, Dahlgren et al. 1999, Lenihan 1999). *Paguristes tuberculatus* is highly mobile, and the constant perturbation to the sediment arising from both the

movement and feeding activity of *P. tuberculatus*, may potentially create an unstable and unsuitable environment for sedentary polychaetes, especially those families that burrow. Previous research documenting reduced densities of sedentary polychaetes (ascribed to sediment destabilization) has been directed at fauna that produce extensive burrows and/or are perceived to invoke large sediment disturbances such as the Callianasids (Pillay et al. 2007a, b). Admittedly, *P. tuberculatus* is highly unlikely to invoke similar levels of disturbance or sediment destabilization to such burrowing, but the species is certainly capable of mobilizing and destabilizing the top 30 mm of sediment. Such a perturbation, albeit small in comparison to Callianasids, may potentially contribute to mortalities of worms when burrows were smothered or filled in, or when burrowing polychaetes were inhibited by greater metabolic demands accredited to maintaining the burrow entrance.

This experiment clearly indicated that whether screwshells are alive, dead or containing hermit crabs each have their own unique impacts in which the abundances of certain species or functional groups may increase or decrease. However, irrespective of the specific differences between the different treatments, the important fact remains that the results provide increased confidence that impacts of *M. roseus* does not depend on the screwshell being alive, and that significant impacts are likely to occur beyond the life-span of live screwshells.

2.5.2 RELATIONSHIP BETWEEN SCREWSHELL DENSITY AND STATE, SEDIMENT STRUCTURE AND INFAUNAL COMMUNITY STRUCTURE.

The presence of screwshells clearly led to alteration of sediment size structure. Treatments with screwshells at high densities exhibited greater proportions of finer sediments (<125 μm) than those with screwshells at low densities or the controls without screwshells. Further, there was some evidence that the treatments of live screwshells exhibited higher quantities of finer sediments (<125 μm) than other types of accumulations at the same screwshell density. Increased substratum rugosity caused by the presence of dense screwshell mats is likely to alter hydrodynamic flow within the benthic boundary layer (Hall 1994, Crooks & Khim 1999, Lenihan 1999, Crooks 2002) and, together with increased complexity of interstitial spaces, promote the accumulation of finer sediments, which become trapped in the coarse-grained interstices between shells and are unlikely to be re-suspended. Further, live screwshells exude vast amounts of biodeposits in the form of pseudo-faeces (Scott 1997, Bax et al. 2003). The deposition of pseudo-faeces is likely to consolidate sediments, trap further quantities of fine silts, alter oxygen levels and increase the organic content and bacterial load of the sediments (Castel et al. 1989, Crooks & Khim 1999, Crooks 2002), all of which may affect infauna.

Accumulation of fine sediments in treatments of screwshells at high densities correlated with variation observed in community structure between treatments. While the correlations between sediment structure and the faunal community were never high (0.26 – 0.28), the BIOENV analysis nonetheless pointed to the finer sediment sizes as those most important in explaining the variation in community

structure between treatments. Sediment size and stability is well recognised as an important factor governing the structure of soft-sediment benthic assemblages (Gray 1974, Rhoads 1974, Reusch et al. 1994, Newell et al. 2001, Gimenez et al. 2006). Therefore, the differences in community structure observed among treatments are likely to be a combination of the direct effects of the physical presence of *M. roseus* and its metabolic requirements, and the indirect effects invoked by alterations to the sediment stability and size structure rather than any one mechanism acting alone.

2.5.3 CAGING EFFECTS

Caging artefacts can make interpretation of results from experiments difficult, as they potentially confound true treatment effects (Hulberg & Oliver 1980, Ross et al. 2003b). Our study used a small PVC fence to maintain the densities of screwshells and hermit crabs throughout the 20 month duration of the experiment. Importantly, there was no evidence of any response to the presence of the fences except for a single species of sedentary polychaete, which exhibited a marginally but significantly higher abundance in fenced controls than in unfenced controls. Importantly, there was no evidence of a fence effect on abiotic functions, with a similar sediment size structure and levels of organic matter in controls with and without fences. Given the minimal differences between fenced and unfenced control areas in this experiment, I am confident that impacts of the PVC fence are negligible, and the results observed among the treatments can be ascribed to screwshell accumulations under natural conditions.

2.5.4 CONCLUSIONS

This study has demonstrated that profound differences exist between communities in patches dominated by *M. roseus* and those associated with soft-sediment patches not supporting screwshells. Generally, the presence of screwshells resulted in higher abundances of select species and functional groups, particularly of epifaunal species utilizing the hard substratum of the shells. Infaunal taxa also exhibited higher abundances in screwshell beds, presumably resulting from both the alteration to sediment size structure and provision of a new 3-dimensional complex habitat. Importantly, the impacts of live screwshells on community structure were distinctly different to those associated with dead and empty screwshells or screwshells occupied by hermit crabs.

This is of particular concern, as it essentially highlights two important facets of the impact of *M. roseus* on native soft-sediment communities. Firstly, impacts are likely to be long lasting, as evidenced by impacts on community structure that exist when accumulations of are dominated by dead shells. The persistence of *M. roseus* shells is high, as they are thick-walled, resistant to predation and do not easily fragment, even in high energy surf zones. Further, the shell's longevity is also likely to be prolonged when utilized by hermit crabs, as the crabs retain the shell above the sediment surface where it is less likely to bio-erode (Hazlett 1981, Reiss et al. 2003). Therefore, impacts of *M. roseus* clearly extend beyond the life of living shells, and the persistent nature of the shells means that the longevity of impacts is likely to be very high.

Secondly, the impact of *M. roseus* on sediment structure and faunal composition of the native benthic community is likely to vary spatially and temporally depending on the dominant screwshell 'states' within a given shell accumulation. For example, newly invaded areas which consist almost totally of living screwshells will exhibit an increasing abundance of epifauna, decreasing abundance of filter-feeding molluscs and an increasing density of predatory gastropods. Alternatively, in depositional zones, which are constituted solely of dead shells, the structure of the community will likely reflect a diverse epifaunal community (after several seasons of natural recruitment) and a diverse mollusc and crustacean dominated infauna. Further, in areas where dead and empty shells are utilized by hermit crabs, the faunal community will also exhibit declining abundance and density of sedentary polychaetes. Therefore, not only are impacts of *M. roseus* likely to last for extensive periods of time, but they are fundamentally dependent on the dominant screwshell state in the impacted area at the time.

Given that *M. roseus* has potentially occupied extensive areas, across a variety of habitats and for a long period, it is likely that the species has already altered the community structure and sediment composition of recipient habitats in SE Australia. Should *M. roseus* continue to expand and invade new areas, significant alteration or 'engineering' to both the physical structure of the benthos, and the community structure of soft-sediment assemblages will inherently occur.

CHAPTER 3

IMMEDIATE AND LONG TERM IMPACTS OF AN INVASIVE ECOSYSTEM ENGINEER ON COMMUNITY METABOLISM

3.1. ABSTRACT

While understanding of the immediate impacts of non-indigenous species in the marine environment is building steadily, knowledge of long term effects and effects on community functioning remains limited. The impacts of *Maoricolpus roseus*, a non-indigenous mollusc inadvertently introduced into Australian waters *ca.* 90 years ago, were assessed using a caging experiment in SE Tasmania. Treatments of living *M. roseus*, dead and empty *M. roseus* shells, and dead *M. roseus* shells occupied by hermit crabs, all maintained at both low (200 m^{-2}) and high (1500 m^{-2}) densities, were applied to *in situ* experimental plots for 20 months, after which community metabolism in the different treatments was assessed using data-logging respirometry chambers. High densities of live *M. roseus* exhibited the highest community respiration (GCR), utilising 697.31 ± 36.47 mmol O_2 0.25 m^{-2} day^{-1}, almost 3 times higher than in control plots without *M. roseus* (257.47 ± 43.26 mmol O_2 0.25 m^{-2} day^{-1}). The high metabolic rate reflected a higher biomass of both infauna and epifauna in treatments with high densities of *M. roseus* compared to control plots. Gross primary production (GPP) also was highest in treatments with high densities of screwshells, irrespective of whether the shells were alive, dead or supporting

hermit crabs. This is because a high biomass of both micro- and macro-algal primary producers developed in treatments containing screwshells. Plots with high densities of *M. roseus* produced between 329.39 (± 37.48) and 384.71 (± 45.71) mmol O_2 0.25 m^{-2} day^{-1} compared with 95.12 (± 30.54) mmol O_2 0.25 m^{-2} day^{-1} in control plots. Screwshell state also had a significant effect on net flux and the GPP/GCR ratios. Communities with live *M. roseus* consumed significantly more oxygen compared to those associated with dead shells or shells occupied by hermit crabs. Rather than reflect the effects of screwshells on infauna and epifauna, the impacts on metabolism appeared to be largely driven by the screwshells themselves and the primary producers living on their shells. Live screwshells were largely responsible for the high respiratory demands, whilst the increase in area of hard substratum provided for producers by the presence of the shells themselves (whether dead or alive) was responsible for effects on rates of primary production. This study demonstrates a dramatic effect of *M. roseus* on community function that is dynamic in nature as screwshell accumulations change from mostly live to mostly dead shells, whether occupied by hermit crabs or not.

3.2. INTRODUCTION

The introduction of non-indigenous species (NIS) remains one of the major threats to the integrity, diversity and health of natural marine ecosystems globally (Carlton et al. 1990, Carlton & Geller 1993, Carlton 1996b, a, Cohen & Carlton 1998, Ruiz et al. 1999, Ruiz et al. 2000, Crooks 2002, Ross et al. 2002, 2003b, a, Ruiz & Hines 2004). Species of particular concern are those capable of both extensively expanding their range following introduction, and establishing at high densities across a variety of habitat types. If these species instigate profound alterations to the structure and function of native assemblages, as well as to the physical habitat, they are often referred to as 'ecosystem engineers' (Jones et al. 1994, 1997, Crooks 2002). Ecosystem engineers in marine environments are capable of drastically altering sediment composition and stability as well as ecosystem processes such as system-level flows of materials, productivity, the quality and quantity of food resources, and boundary layer processes such as nutrient cycling and metabolic fluxes (Jones et al. 1994, 1997, Schwindt et al. 2001, Crooks 2002). Moreover, these species are often capable of controlling the availability of resources through manipulation of the physical state of biotic or abiotic components of the environment (Schwindt et al. 2001, Crooks 2002).

The impacts of invasive ecosystem engineers are usually identified as reflecting one of three primary mechanisms (Vitousek 1990, Crooks 2002). First, NIS may utilize resources (particularly nutrients) in a different manner to native species such that the change in biogeochemical cycling in turn affects the availability and flow of these resources to other species. Second, NIS can alter the transition of biomass or energy

by changing the intricacies of a particular food web. Third, the NIS may affect disturbance regimes, effectively governing the availability and quality of physical and abiotic resources. NIS that impact ecosystems through any of these mechanisms threaten the integrity and functioning of native ecosystems by interfering with both the biotic and abiotic resources that fundamentally characterize the ecosystems themselves (Jones et al. 1997, Crooks 2002).

Molluscs in particular have been highly successful invaders of marine and freshwater environments, and many are recognized as ecosystem engineers. For example, the Pacific oyster (*Crassostrea gigas*), Zebra mussel (*Dreissena polymorpha*) and the Japanese mussel (*Musculista senhousia*) all have the capacity to drastically alter the habitat characteristics of their recipient environments and, in turn, the structure of their respective communities (Castel et al. 1989, Stewart & Haynes 1994, Crooks 1998b, Crooks & Khim 1999, Horvath et al. 1999).

Australia also supports some highly invasive non-indigenous molluscs, including the New Zealand Screwshell (*Maoricolpus roseus*), a turritellid gastropod inadvertently introduced to Tasmania during the 1920s, most likely accompanying shipments of live oysters (Bax et al. 2003). *Maoricolpus roseus* has become among the most widespread of Australia's exotic marine species, resident on the coast between the latitudes of 43° 39'S and 34°00'S , with the majority of high-density aggregations occurring off Victoria, in Bass Strait and in south-eastern Tasmania (Allmon et al. 1994, Gunasekera et al. 2005, Nicastro et al. 2009). In its native range of New Zealand, *M. roseus* occupies a variety of habitat types from soft-sediments to

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exposed rocky habitats over a depth range of 0 - 200 m. In Australia, *M. roseus* occupies a similar range of habitats from muddy silts to rocky reef, although it is most common on shelly substrata and coarse sands (Bax et al. 2003, Reid 2003). Screwshell accumulations regularly attain densities of 600 - 1200 m^{-2} (Allmon et al., 1994), and up to ~ 2500 m^{-2} (Reid, 2003), with most aggregations consisting of both live and dead shells. Depending on the age of the accumulation, the majority of dead shells may contain hermit crabs. Given that *M. roseus* can occupy vast areas of sea floor across a wide range of habitats, and at very high densities, the potential exists for *M. roseus* to create a highly engineered environment in which faunal composition, nutrient cycles, energy flow, and abiotic habitat characteristics such as sediment size structure and stability, are likely to be profoundly different to those in otherwise similar non-invaded soft-sediment habitats.

Research into impacts of NIS on soft sediment communities, particularly those that engineer the habitat in some way, has usually focused on alterations to habitat or community structure (e.g. Castel et al. 1989, Stewart & Haynes 1994, Creese et al. 1997, Crooks 1998a, Crooks & Khim 1999, Horvath et al. 1999, Strayer et al. 1999b, Hedge & Kriwoken 2000, Schwindt et al. 2001). In soft-sediment habitats, this research usually involves comparing areas of the benthos with and without the NIS, or artificially manipulating small patches of the introduced species to assess impacts on infaunal community structure in general, or on selected species of particular interest. However, alterations to ecosystem function, particularly to the flow of nutrients and energy, are also an important element in defining impacts (Vitousek 1990, Crooks 2002). While it is generally inferred that dramatic

alterations to native habitat and/or community structure induced by NIS are likely to have fundamental impacts on community function (e.g. community metabolism, nutrient flux), few studies have attempted to directly quantify impacts on community function. However, evidence from the role of types of native ecosystem engineers highlight the potential for major effects of NIS on ecosystem processes (Webb & Eyre 2004a, Hewitt et al. 2006, Norling & Kautsky 2007). Clearly then, quantifying impacts of NIS on both community structure and community function in parallel will undoubtedly produce a more comprehensive and robust estimate of overall impact.

Impacts of *M. roseus* on the metabolism of native soft-sediment communities in south east Tasmania were quantified using an experiment in which manipulate patches of screwshells were maintained *in situ* at densities commonly attained under natural conditions. Metabolism was estimated using custom-designed metabolic chambers. The separate effects of the different screwshell states (i.e. live screwshells vs. dead screwshells vs. dead screwshells containing hermit crabs) at two densities (high vs. low) were assessed, and differences in metabolism between these treatments interpreted in terms of infaunal and primary producer biomass, and the overall composition of the benthic community.

3.3. METHODS

3.3.1 STUDY SITE

The work was conducted in a shallow sheltered embayment in south east Tasmania, Australia (Bligh Pt., D'Entrecasteaux Channel, Fig 3.1). The deeper region adjacent to Bligh Point (12 m) is soft-bottom habitat consisting of fine and coarse sands and accumulations of shell grit. While Bligh Pt. supports only sparsely scattered, low-density (10 m^{-2}) patches of *M. roseus*, the site exhibits similar sediment, depth, light and flow characteristics to other nearby embayments supporting screwshells at high densities. Compared with those bays, the impact of the very low density of *M. roseus* at Bligh Pt. is likely to have been negligible.

3.3.2 EXPERIMENTAL PROTOCOL AND CHAMBER DESIGN

A detailed description of the experimental design is given in Chapter 2. In summary, treatments included 3 levels of substratum type (live screwshells, dead and empty screw shells, and dead screwshells with 50% occupancy by hermit crabs) crossed with 2 levels of screwshell density (200 m^{-2} and 1500 m^{-2}). The treatments were devised to represent different screwshell 'states' observed patchily distributed throughout the benthic habitat. Treatments were enclosed and maintained by 0.75 m x 0.75 m x 90 mm high polyvinyl chloride (PVC) frames. 'Controls' comprised of PVC frames over unmanipulated areas without screwshells, and unmanipulated areas without either PVC frames or screwshells. Four replicates of each treatment were positioned randomly on the sea floor in an area 20 x 20 m. The experiment was maintained for 20 months until August 2007 at which time, metabolic chambers

were deployed over each experimental plot for 22 hours, including both a night (dark) and day time (light) period within each incubation.

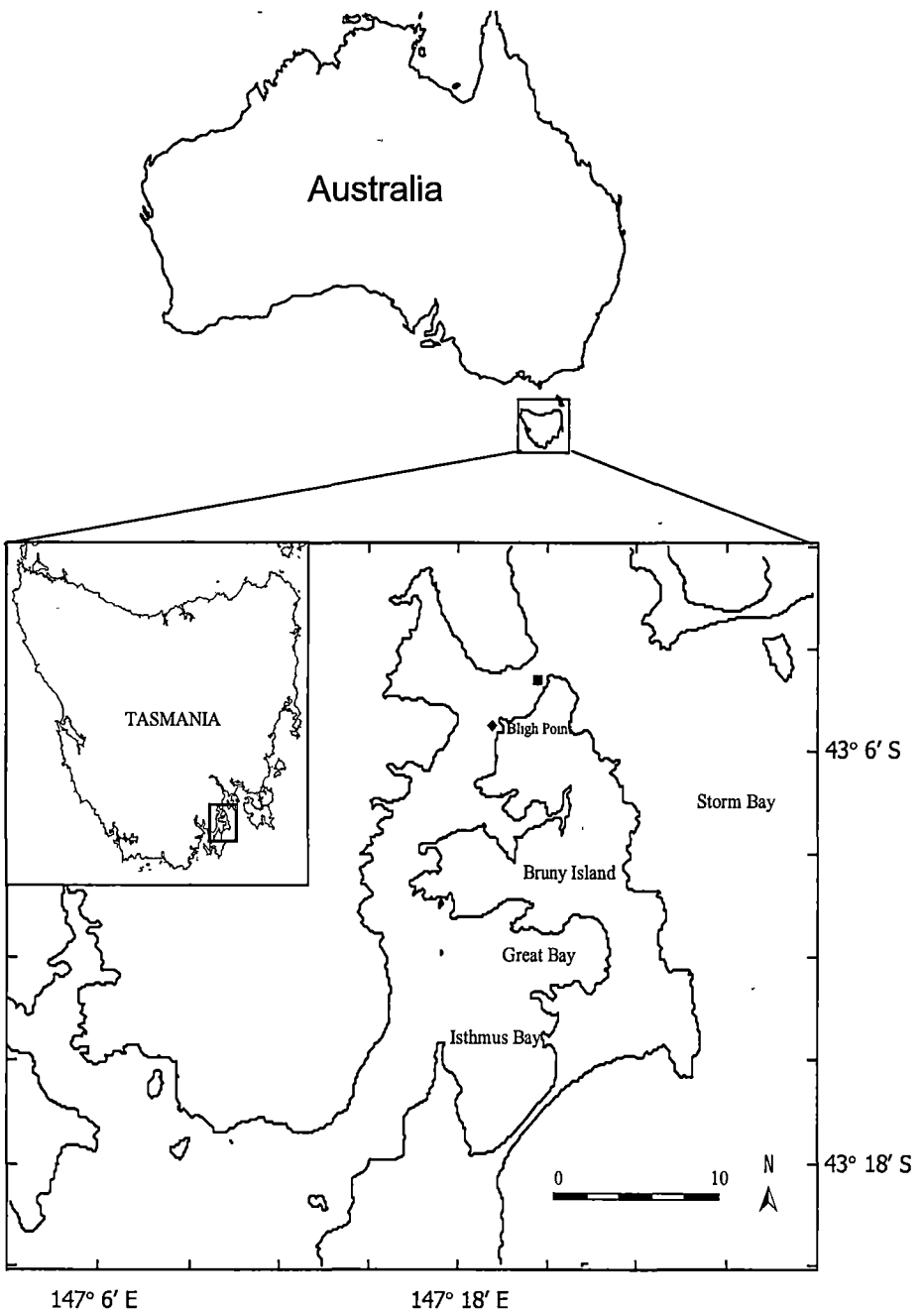

Figure 3.1. Map of the D'Entrecasteaux Channel showing the location of the experimental study site at Bligh Point (◆) and the screwshell collection site at Dennes Point (■).

Each chamber consisted of a transparent polyvinyl chloride (PVC) cylinder, 300 mm in internal diameter and 250 mm high, sealed at one end with a PVC roof and chamfered at the other to minimise resistance during insertion into the sediment (Fig 3.2). Circulation within the chamber was via a magnetic stirrer attached to the chamber roof. The stirrer, driven by a 9 V DC motor, rotated at *ca.* 8 rpm. Rulers mounted on the sides of each chamber enabled the depth of insertion into the sediment, and thus the internal volume, to be calculated. Inserted through the roof of each chamber was an optical dissolved oxygen (DO) probe (Aanderaa oxygen optode 4130), which sensed DO concentration and water temperature every 10 mins, writing to a data logger mounted separately to the chamber in a submersible housing (Ikelite). The data logger was a Tattletale TFX 1-11.v2 and associated prototype board (Onset computer corp.), enabling each chamber to be operated independently.

Photosynthetically Active Radiation (PAR) adjacent to the plots was also measured using two underwater quantum sensors (Li-cor LI-192SA). Activation of the PAR sensors was also controlled by the TFX 1-11.v2. For the 10 min interval between DO readings, the PAR sensor was activated every two minutes, and the averages of the five 2-minute readings stored on the TFX 1-11.v2. This allowed impacts of cloud cover and shading from nearby shores to be detected, which otherwise may have been overlooked by taking PAR readings at 10 min intervals. PAR was recorded throughout the entire incubation.

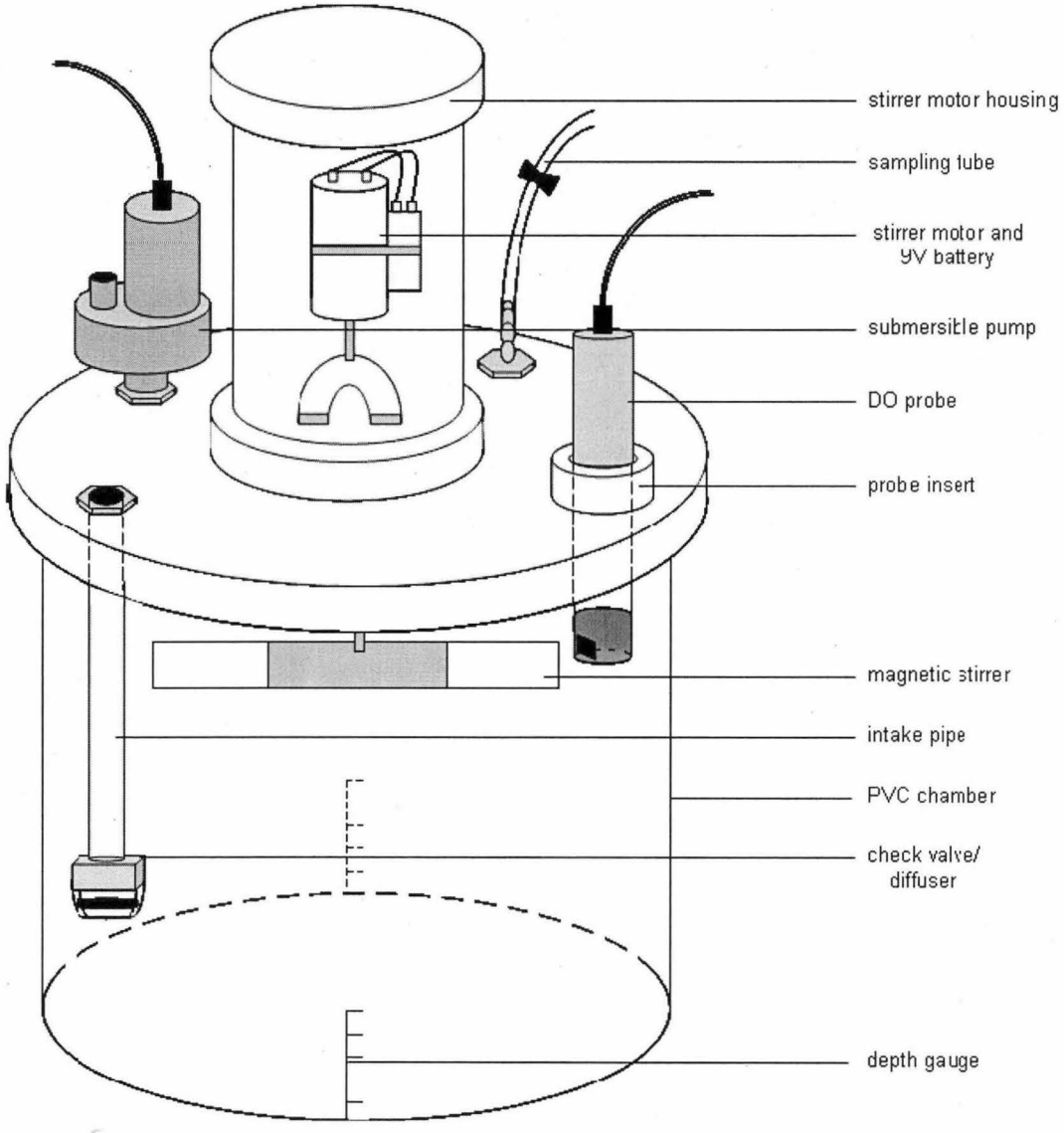

Figure 3.2. Diagram of the chamber design; chamber dimensions are 250 mm in height and 300 mm in internal diameter.

3.3.3 DETERMINATION OF PRIMARY PRODUCER AND INFAUNAL BIOMASS

On completion of chamber incubations, three sediment cores (30 mm diameter x 80 mm long) were extracted from each plot, from which the biomass of microphytobenthos (MPB) biomass was calculated. Cores used for MPB (measured as *Chl a*) were stored at -80 °C and processed within 2 weeks of collection. MPB biomass was calculated using a 90 % acetone extraction on the upper 5 mm of each core, including quantifying phaeophytin after acidification with 0.1 M HCL, and conducting spectrophotometry on the extracts (after Strickland & Parson 1972). Note that I employed a hexane extraction method (after Whitney & Darley 1979), which quantifies chlorophyll degradation products, for a subset of the cores, however because so few degradation products (2-5 % in each sample) were detected using this method, it was appropriate to use only the acetone extraction for the remainder of the cores. In experimental plots containing screwshells, random samples of 12 screwshells were collected and processed for epiphyte biomass, also using acetone extraction. These shells were also stored at -80 °C and processed within 2 weeks of collection.

After all cores were taken, all screwshells (and associated epifauna) were gently collected by hand from those treatment plots containing shells and fixed in a buffered 5 % formalin solution. Each plot was then suction - sampled to a depth of 100 mm using an air-driven suction device which collected the contents of each plot in to individual bags of 1 mm mesh. Freshly collected material was fixed in a 5 % formaldehyde solution with Rose Bengal stain and stored for identification. In the laboratory, epifauna attached to the screwshells were counted and removed to 70 %

alcohol. Infaunal samples were sorted initially over a series of 4 mm, 2 mm and 1mm mesh sizes. All infauna from the 4 mm portion were counted, however, to cope with the volume of the 2 mm and 1 mm fractions, they were split using a Jones-style riffle splitter into quarters, and two of these sub samples analyzed. All epifauna and infauna from the sieve fractions were removed to 70 % alcohol, counted and weighed (wet) using a balance accurate to 0.01 g in order to quantify infaunal biomass. Epifauna was estimated from counts, as the inability to adequately remove all epifaunal taxa physically attached to the screwshells (stone corals, bryozoans etc.), prohibited quantification of their biomass as wet weights.

3.3.4 TESTING FOR ARTEFACTS

When using closed chambers to quantify community metabolism, artefacts can arise if conditions within the chamber become different to those experienced by the community under natural circumstances. For example, oxygen concentration within the chamber can fall due to the metabolic demands of the encapsulated community. Soft-sediment communities isolated in this way for extended periods of time are likely to experience declines in dissolved oxygen (DO) concentration, and so the possibility of negative impacts on infauna with depleted DO concentrations as an experimental aberration, must be addressed.

To assess whether communities were affected by reductions in DO concentration experienced over the incubation period, chambers were deployed in pairs in a random subset of treatment plots. One of the chambers was fitted with a small 12 V DC bilge pump enabling the chamber to be flushed at frequent intervals, while the

other was a 'standard' chamber without a pump. The submersible pump was positioned on the roof of the chamber and pumped water from within the chamber to the outside. The water removed was replaced through an intake mounted opposite the pump, also in the chamber roof. The intake was coupled with a check valve which acted as a diffuser, allowing incoming water to disperse across the bottom of the chamber without disturbing the sediment or boundary layer processes (Fig 3.2). Optimal flushing (100% clearance of chamber water and no disturbance of sediments as observed in dye studies) was achieved by positioning the diffuser 50 mm above the sediment surface and using a pump rate of 3 $L.min^{-1}$ for 20 mins. Incubations using paired chambers were carried out over 4 hour periods. Paired chambers were deployed in 10 randomly selected treatment plots (over a range of screwshell densities and states) and the flux estimates calculated from the flushed chambers (which DO levels were never less than 85 % of the ambient concentration) were compared to those derived from unflushed chambers (where DO declined linearly for the duration of the incubation, typically to between 40-60% of ambient, depending on the treatment). Observation of highly linear patterns in oxygen utilisation, and essentially identical rates of oxygen flux over the entire incubation period in both the flushed and unflushed chambers installed on the same community, suggests that the community did not respond in any significant way to the changing oxygen concentration within the chambers over the incubation period.

The potential for 'caging' artefacts also needed to be addressed because the experiment used a small PVC fence to maintain densities of shells within treatment

plots. Therefore, comparisons were made between the fenced and unfenced controls in all measured parameters to test for effects of the PVC fencing.

3.3.5 DATA COLLATION AND STATISTICAL ANALYSES

Incubations at night gave rise to estimates of respiration per hour, which were extrapolated to full day estimates of gross community respiration (GCR) by multiplying estimates by 24 (24 hours per day). Primary production per hour was calculated as the difference between day (light) and night (dark) incubations. Community primary production (GPP) was calculated by multiplying the hourly rate by 7 hrs and 45 mins, which was the length of luminous hours determined from the PAR quantum sensors. GCR and GPP were calculated assuming the absence of a diel signal in respiration. All data were checked for non-linear trends which would indicate feedbacks arising from altered oxygen concentrations within the chamber.

Differences among treatments in respiration, primary production, net oxygen flux, and the biomass of primary producers and infauna were all assessed using fixed effects Analysis of Variance (ANOVA). The model included the fixed effects of 'screwshell density' (2 levels: high/low), crossed with 'screwshell state' (3 levels: live screwshells, dead screwshells, and dead screwshells with 50% occupancy by hermit crabs) and the 'screwshell density' * 'screwshell state' interaction. For the ANOVAs, data and residuals were checked for normality and homoscedasticity, and transformed as necessary to stabilize variances depending on the relationship between group standard deviations and means (Draper & Smith 1981). Following overall tests for treatment effects in the ANOVAs, two orthogonal planned

comparisons were conducted. Firstly, the fenced control (C+F) was compared to all plots containing screwshells at high densities (H), and secondly, the fenced control was compared to all plots containing low densities of screwshells (L). Since these contrasts are orthogonal, no adjustment to the type I error rate (α) was required. All ANOVAs were conducted using the SAS 9.1 statistical software (Statistical Analysis System).

To assess the possibility of chamber artifacts influencing community metabolism, DO concentrations in paired flushed and unflushed chambers were compared. Because incubations in flushed chambers lasted 4 hours (i.e. the pump activated every 4 hrs), comparisons were made across six consecutive incubations in a given 24 hour period; 1 afternoon incubation, 4 night incubations and 1 morning incubation. A linear regression was fitted to the difference in flux rates between paired chambers from all six incubations. An intercept of zero would indicate no differences in DO rates flux between flushed and unflushed chambers, while a zero slope would indicate that any difference in flux rates between chambers was constant throughout the full 24 hr period of the incubation. Regressions were fitted using the SAS 9.1 statistical software.

To test for artifacts in using PVC frames to contain the screwshells, results from fenced (C+F) and unfenced controls (C-F) were compared using 1-way ANOVAs. Lack of significant differences between C+F and C-F plots indicated negligible artifacts associated with the use of the PVC frames, enabling unambiguous interpretation of the main treatment effects.

3.4. RESULTS

3.4.1 COMMUNITY METABOLISM

Treatment plots supporting high densities of screwshells, irrespective of whether screwshells were alive, dead or supporting hermit crabs, exhibited significantly higher community primary production (GPP) than treatments with low densities of shells, and the controls (Fig 3.3a, Table 3.1). GPP from all low density treatments did not differ significantly to the control plots (Fig 3.3a, Table 3.1). There was no significant effect of screwshell state (i.e. live screwshell, dead screwshell and hermit crab treatments) on GPP at either low or high densities.

Treatment plots supporting high densities of screwshells also exhibited significantly higher community respiration (GCR) than treatments with low densities of shells and the controls (Fig 3.3b, Table 3.1). There were also significant differences in GCR between the different screwshell states. Within the high density treatments, rates of respiration in communities supporting live screwshells were 33 % faster than communities with dead screwshells and 38 % faster than treatments with dead screwshells containing hermit crabs (Fig 3.3b). Differences between the different screwshell states across the low density treatments were less obvious and no significant differences were detected (Fig 3.3b, Table 3.1)

The net oxygen flux for the 24 hr incubation period across all of the treatments was always negative, indicating that GCR always exceeded GPP irrespective of the treatment (and including the controls, Fig 3.3c). Despite the high rate of GPP in the high density/live screwshell (HL) treatment, the GCR rate far exceeded GPP in this

treatment. In fact, the HL treatment had the highest negative net O_2 flux, significantly higher than all other treatments (Fig 3.3c, Table 3.1). The smallest net negative flux was observed in the controls. Interestingly perhaps, dead shells at high densities (HD) and high density hermit crab (HHC) treatments exhibited significantly smaller net negative flux than the HL treatment, but the same as the low density treatments. Unlike the HL treatment, GCR rates were not as high in these two treatments, which combined with the very high rates of GPP, led to reduced net DO consumption when compared to the HL treatment (Fig 3.3).

Although the net oxygen flux is indicative of how the opposing processes of respiration and production interact, another useful representation of overall community metabolism is the GCR:GPP ratio (Odum 1969). There are 4 key points that are highlighted from results for the GCR:GPP ratio. Firstly, the GCR:GPP ratio for all treatments was <1, again indicating that respiration exceeded primary production in all treatments. Secondly, treatments with high densities of screwshells yielded a higher GCR:GPP ratio than those with low densities, indicating that these treatments exhibited very high GPP, despite also having a much higher GCR than the treatments with low densities of screwshells (Fig 3.3). Thirdly, the GCR:GPP ratio in the low density treatments was not significantly different to controls, indicating that effects on community metabolism at low densities of shells are minimal, and not dependent on screwshell state. Lastly, the HL treatment exhibited a lower GCR:GPP ratio than the other high density treatments (HD and HHC) indicating that while GPP was similar across the treatments with high densities of screwshells, the HL treatment exhibited a much higher GCR (Fig 3.3).

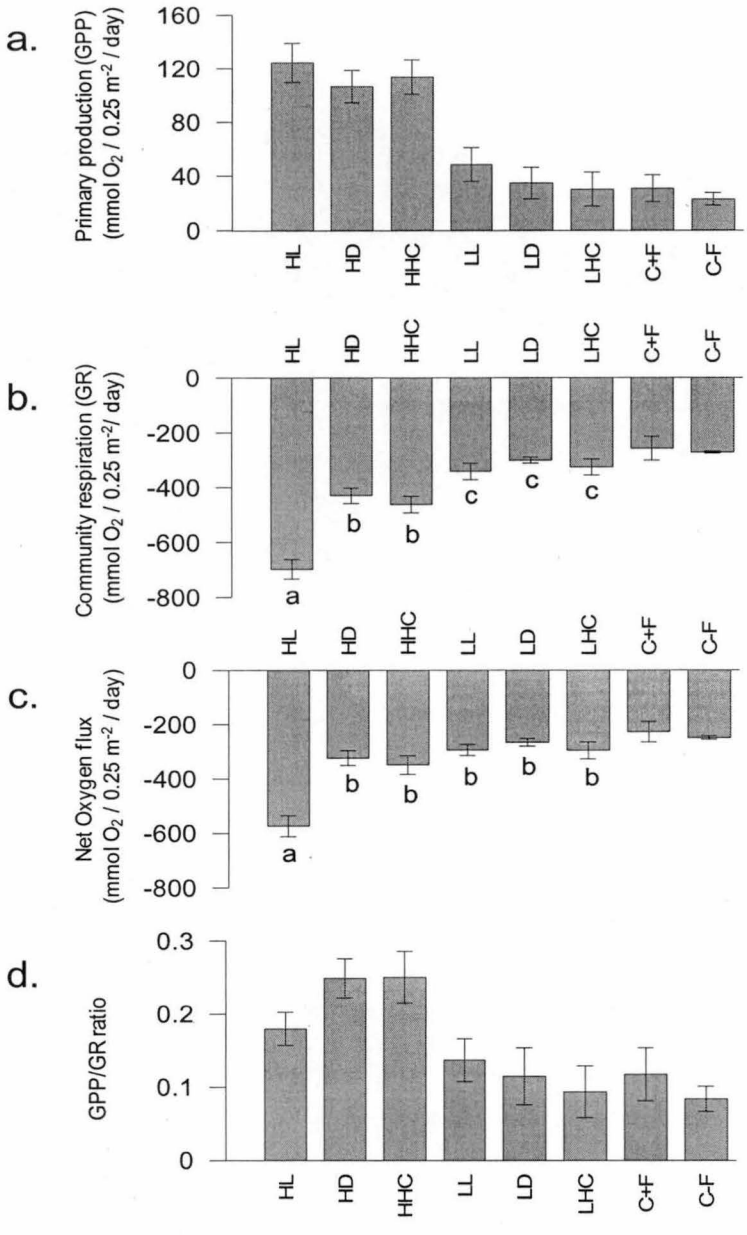

Figure 3.3. Gross primary production (a), respiration (b), and net oxygen flux (c) over a 24 hour period, and overall community metabolism represented as the GPP/GCR ratio (d) across all treatments and controls. GPP/GCR is the ratio of gross primary production to gross community respiration. All estimates are means (± S.E.) calculated from n=4 replicate plots of each treatment. Treatments are denoted as: HL = high density/live screwshells; HD = high density/dead screwshells; HHC = high density/hermit crabs; LL = low density/live screwshells; LD = low density/dead screwshells; LHC = low density/hermit crabs; C+F = fenced control; C-F = unfenced control. REGWQ groupings from significant density*state interactions in the main analysis are represented by the same letters positioned above the respective treatments. Controls were assessed *a priori* and independently of the primary analysis, and therefore are not included in the REGWQ groupings.

Table 3.1. Results of Fixed effects ANOVA among screwshell treatments for metabolic fluxes, primary producer biomass, infaunal biomass and epifaunal abundance. Results are of overall ANOVAs comparing among treatments of different screwshell states and densities, and the planned comparisons C+F vs. H and C+F vs. L test for the effects of screwshell density with regards to the controls (no screwshells) and C+F vs. C-F test for caging effects. Significant P values are shown in bold face (α= 0.05). Treatments are denoted as: C+F = fenced control; C-F=unfenced control; H=high density; L=low density.

	Main analysis				Planned comparisons					
					Density comparisons				Fence comparison	
		P values			CF vs. H		CF vs L		CF vs CNF	
Variable	MS_{resid}	State	Density	State*Density	MS_{resid}	P value	MS_{resid}	P value	MS_{resid}	P value
Degrees of freedom	18	2	1	2	12	1	12	1	6	1
Metabolic fluxes										
Respiration (GR)	7403513.0	**<0.01**	**<0.01**	**<0.01**	10999153.0	**<0.01**	8513483.7	0 09	8471114.9	0 75
Production (GPP)	652 3	0.41	**<0.01**	0.90	625 1	**<0.01**	547.9	0.61	237.9	0.50
Net O2 flux (NF)	3375.3	**<0.01**	**<0.01**	**<0.01**	4928.5	**<0.01**	3013.7	0 09	2957.8	0 58
GR GPP ratio	0 1	0.76	**<0.01**	0 19	0.1	**<0.01**	0.1	0 96	0.1	0.43
Primary producer biomass										
Total Chla	71054.2	0.58	**<0.01**	0.96	12983.4	**<0.01**	92162 7	**<0.01**	8111 1	0.19
Shell Chla	11669 7	0.08	**<0.01**	0.13	16521.5	**<0.01**	983.0	**<0.01**	N/A	
Sediment MPB Chla	69078.8	0 29	**<0.01**	0.63	7384.8	**<0.01**	0.1	0.10	8111 1	0.19
Total Phao	8088.4	**0.02**	**<0.01**	0 83	6959.7	**<0.01**	10249.6	**<0.01**	22269.4	0.08
Shell Phao	402.2	0.61	**<0.01**	0.16	589.4	**<0.01**	13.9	**<0.01**	N/A	
Sedimnet MPB Phao	21370.7	0 92	**<0.01**	0.77	25683 7	**<0.01**	11449.0	0.17	22269.4	0.08
Infaunal biomass										
Total infauna	4.9	0.98	0 16	0 77	4.7	0.06	2.7	0.20	1.0	0.16
Molluscs	1.6	0.20	0.41	0.58	1 5	0 82	1.2	0 35	1.3	0.79
Polychaetes	0.1	**<0.01**	**<0.01**	0.16	0 1	**0.05**	0 2	0 87	0.1	0.10
Crustaceans	1.2	0.58	0.11	0.18	0 9	**0.02**	1.0	0 23	1.3	0.79
Echinoderms	12.4	0.78	0 22	0.94	16.9	0 71	8.1	0.59	6.6	0 22
Epiphyte abundance										
Stone corals	300 5	0.10	**<0.01**	0.15	64.1	**<0.01**	54.7	**<0.01**	109.6	0 31
Bryozoans	143.9	0.32	**<0.01**	0.45	203 7	**<0.01**	12.4	**<0.01**	1 6	0.30
Chitons	5 0	0.84	**<0.01**	0 35	4 9	0 07	4 8	0.17	2 3	0 06

3.4.2 BIOMASS OF PRIMARY PRODUCERS AND INFAUNA

Primary producer biomass (PPB) in the form of sediment microphytobenthos (MPB) and shell epiphytes (usually filamentous algae) also differed among treatments. Plots with high densities of screwshells supported the highest total biomass of primary producers (estimated as Chl *a*), yielding between 2.76 – 2.89 mg Chl *a* 0.25 m^{-2} plot (Fig 3.4). The low density treatments supported significantly less PPB (between 0.97 – 1.15 mg Chl *a* 0.25 m^{-2} plot), but were marginally higher than both the fenced and unfenced controls (total PPB of 0.63 mg Chl *a* 0.25 m^{-2} plot and 0.73 mg Chl *a* 0.25 m^{-2} plot respectively) (Fig 3.4, Table 3.1).

The higher total PPB associated with high densities of screwshells is indicative of both a higher biomass of sediment MPB and a higher quantity of shell epiphytes (Fig 3.4). Individual shells from the different treatments support similar amounts of epiphytes, so that significant differences among treatments effectively reflected different densities of shells among treatments (Fig 3.4, Table 3.1). Patterns observed for Chl *a* biomass were also reflected in the biomass of phaeophytin (Fig 3.4)

Clear differences were also evident between treatments in the biomass of the different size fractions of infauna (Fig 3.6), and in the abundance of epifaunal taxa attached to the hard substrata of the screwshells (Fig 3.7). The PCA and associated biplot conducted on data pooled into functional groups indicated clear separation of communities between the different treatment plots (particularly treatments of different screwshell density). This separation was typically governed by the high abundance of epifaunal taxa, particularly stone corals, chitons and bryozoans

associated with high densities of screwshells (Figs 3.5, 3.7). High density treatments also exhibited a higher biomass of infaunal polychaetes and crustaceans, while molluscan infauna was more prevalent in low density treatments and the controls (Fig 3.5, 3.6). While there was a greater density of epifauna and infaunal biomass in plots with high densities of screwshells, there was little evidence that the size structure of organisms differed among treatments, with similar proportions of organisms retained on 4 mm, 2 mm and 1 mm sieves across all treatments and controls (Fig 3.6).

3.4.3 CHAMBER ARTEFACTS AND EXPERIMENTAL CAVEATS

There was no evidence that the presence of the PVC 'fence' used to restrict screwshell dispersal from plots affected oxygen fluxes (Fig 3.3), primary producer biomass (Fig 3.4), or the biomass of infauna (Fig 3.6) or abundance of epifauna (Fig 3.7, Table 3.1). Further, the composition of communities at a broad taxonomic level was similar in fenced and unfenced control plots (Fig 3.5).

The potential for declining oxygen levels in the metabolic chambers to impact functioning of the communities contained therein was assessed by deploying paired chambers within the same treatment plot in which the water in one chamber was completely flushed every four hours, enabling replenishment of depleted oxygen levels, while the other chamber was incubated without flushing for the duration of the 24 hour incubation.

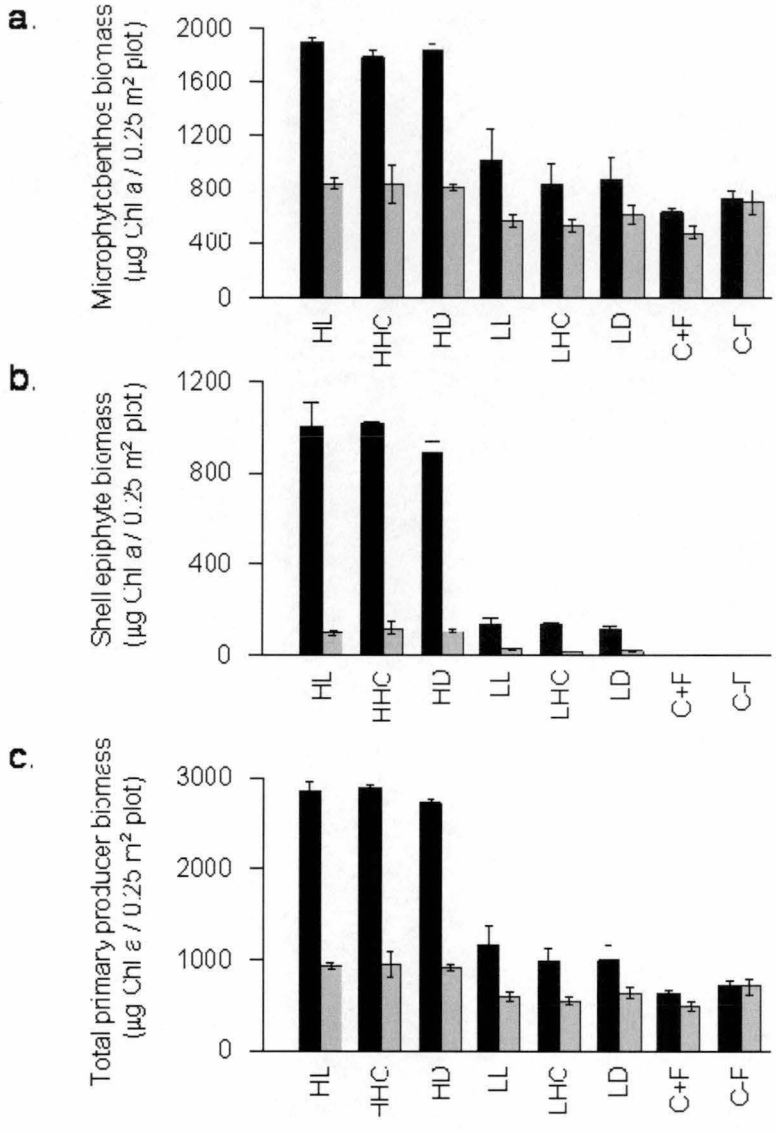

Figure 3.4. Biomass of sedimentary microphytobenthos (MPB) (a), shell epiphytes (b), and total primary producers (c), across treatment plots. All estimates are displayed as mean µg Chl *a* (dark bars) and µg phaeophytin (grey bars) per 0.25 m^2 averaged over n=4 replicate treatment plots. Estimates for MPB were calculated from 3 sediment cores taken from each replicate plot and extrapolated to provide an estimate for the total 0.25 m^2 area of each treatment plot. Shell epiphyte biomass was estimated from 12 randomly selected shells from each treatment plot and estimates are adjusted to account for differences in screwshell density between the different treatments. Total primary producer biomass is a combination of both MPB and shell epiphytes for the total 0.25 m^2 area. Treatments are denoted as: HL = high density/live screwshells; HD = high density/dead screwshells; HHC = high density/hermit crabs; LL = low density/live screwshells; LD = low density/dead screwshells; LHC = low density/hermit crabs; C+F = fenced control; C-F = unfenced control. All data are presented as means (± S.E.) of n=4 replicate plots.

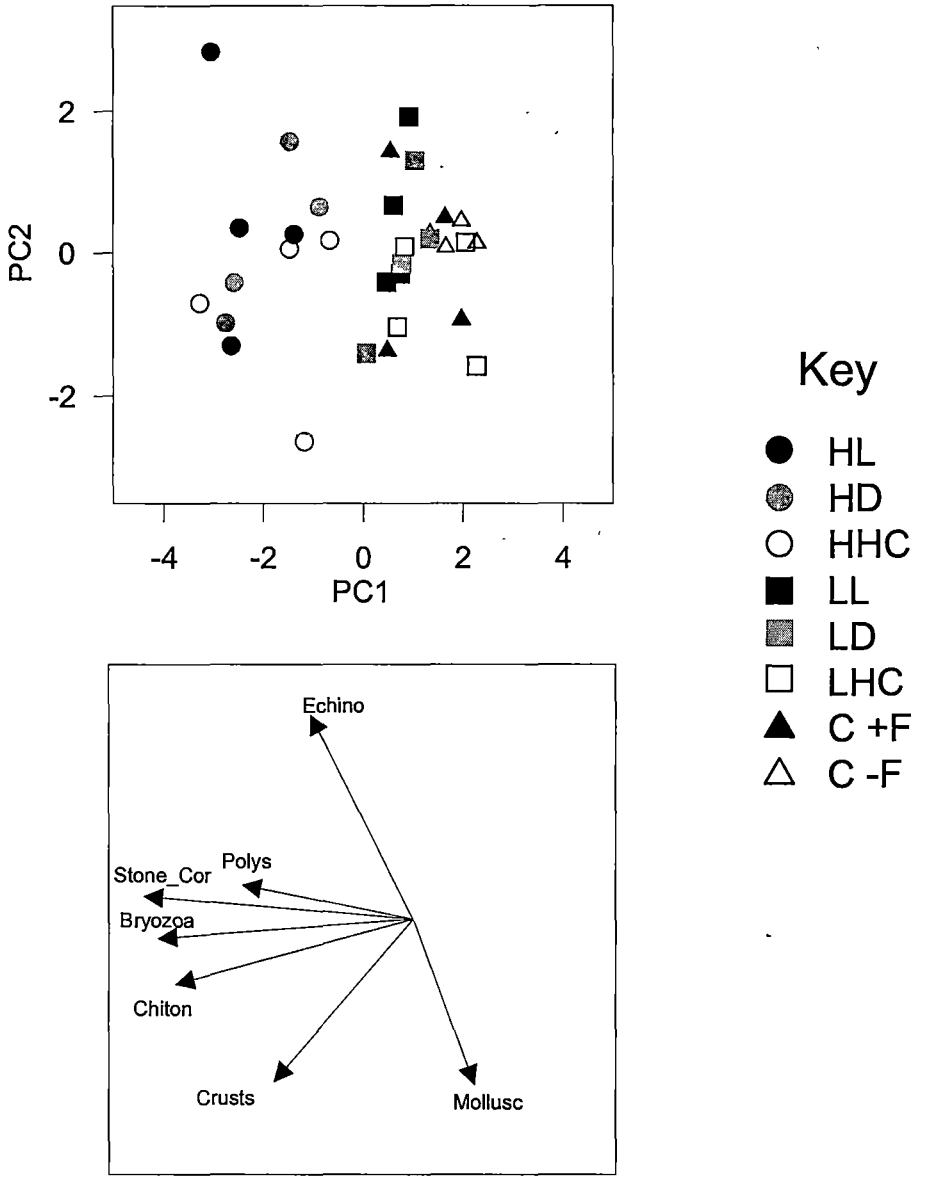

Figure 3.5. PCA ordination and associated biplot indicating the separation of infaunal community structure at a functional group level in treatments depending on screwshell density. All ordinations were based on data reduced to major functional groups for all treatment plots (n=4). The first two principle components accounted for 68.9% of the total variation. The biplot identifies the functional groups most important in shaping the patterns observed in the PCA ordinations. Functional groups include stone corals (Stone_Cor), bryozoans (Bryozoa), crustaceans (Crusts), polychaetes (Polys), molluscs (Mollusc), echinoderms (Echino) and chitons (Chiton). Treatments are denoted as: HL = high density/live screwshells; HD = high density/dead screwshells; HHC = high density/hermit crabs; LL = low density/live screwshells; LD = low density/dead screwshells; LHC = low density/hermit crabs; C+F = fenced control; C-F = unfenced control. All data are presented as means (± S.E.) of n=4 replicate plots.

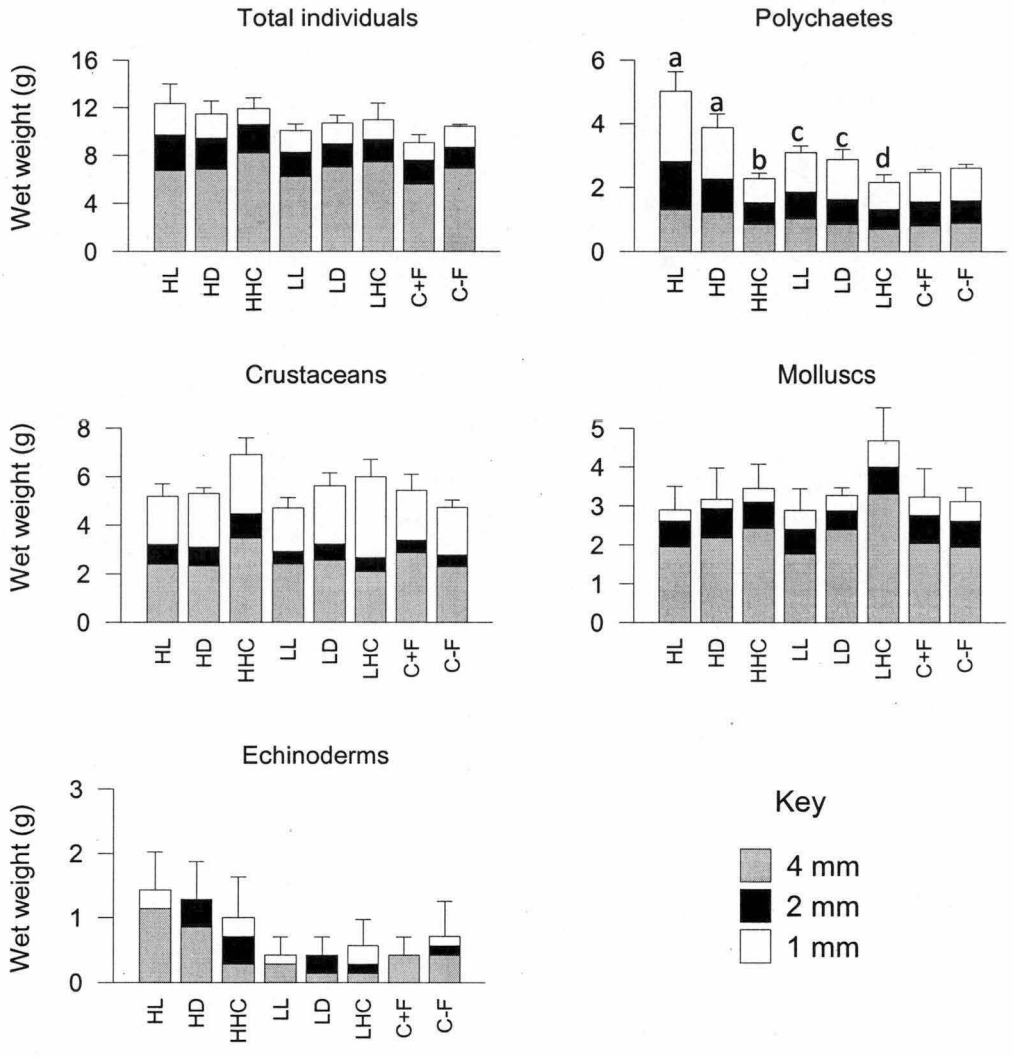

Figure 3.6. Biomass of total infauna, polychaetes, crustaceans, molluscs and echinoderms in each of the treatments. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). Estimates also depict the relative proportions of total biomass retained on 1, 2 and 4 mm sieve sizes. All estimates are a total census of each experimental plot, obtained from a suction sample which was conducted on the whole 0.25 m^{-2} inner plot area. Treatments are denoted as: HL = high density/live screwshells; HD = high density/dead screwshells; HHC = high density/hermit crabs; LL = low density/live screwshells; LD = low density/dead screwshells; LHC = low density/hermit crabs; C+F = fenced control; C-F = unfenced control. REGWQ groupings from significant density*state interactions in the main analysis are represented by the same letters positioned above the respective treatments. Controls were assessed *a priori* and independently of the primary analysis, and therefore are not included in the REGWQ groupings.

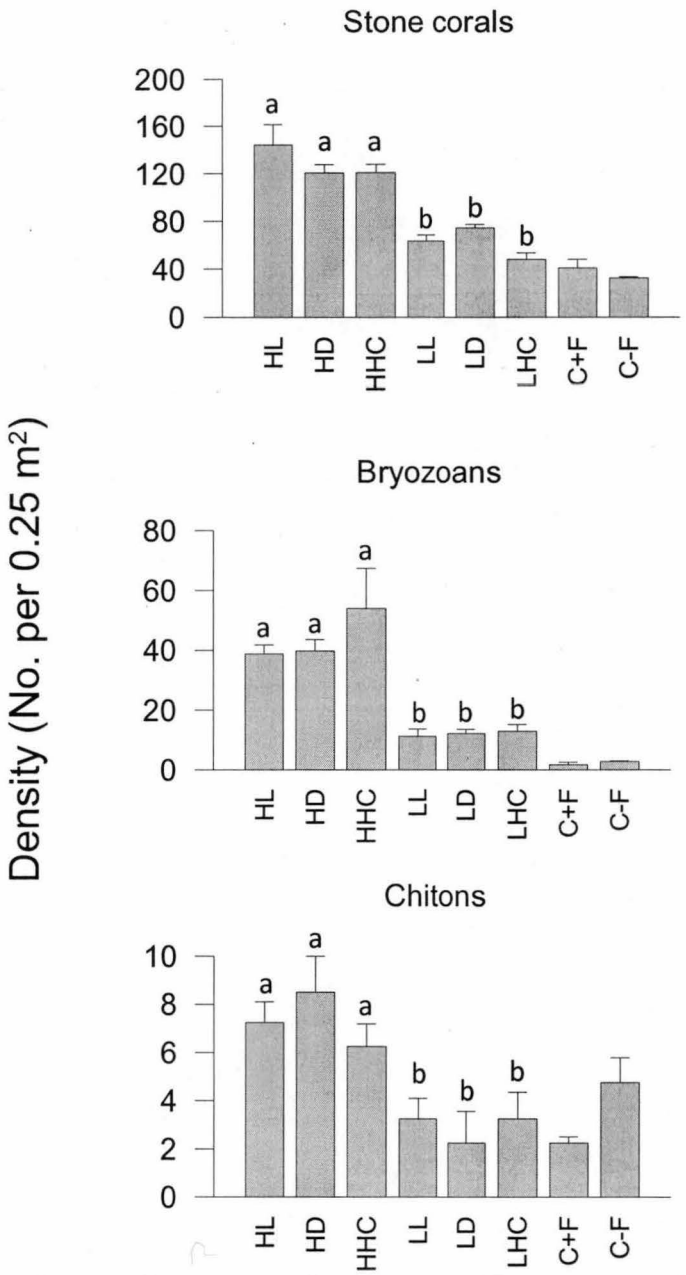

Figure 3.7. Abundances of common epifauna across all treatments. All estimates are averages of n=4 replicate 0.25m^{-2} plots (± S.E.). Treatments are denoted as: HL = high density/live screwshells; HD = high density/dead screwshells; HHC = high density/hermit crabs; LL = low density/live screwshells; LD = low density/dead screwshells; LHC = low density/hermit crabs; C+F = fenced control; C-F = unfenced control. REGWQ groupings from significant density*state interactions in the main analysis are represented by the same letters positioned above the respective treatments. Controls were assessed *a priori* and independently of the primary analysis, and therefore are not included in the REGWQ groupings.

There was no evidence that declining DO concentrations in unflushed chambers negatively impacted the incubated community. DO flux in flushed and unflushed chambers deployed in the same experimental plot were essentially identical, irrespective of how long the incubation went for (Fig 3.8). In a regression fitted to the differences between flushed and unflushed chambers over time, the y-intercept was not significantly different to zero (indicating negligible differences in DO flux between flushed and unflushed chambers) and the gradient was also not significantly different to zero, indicating that DO flux was similar in flushed and unflushed chambers throughout the 24 hour incubations.

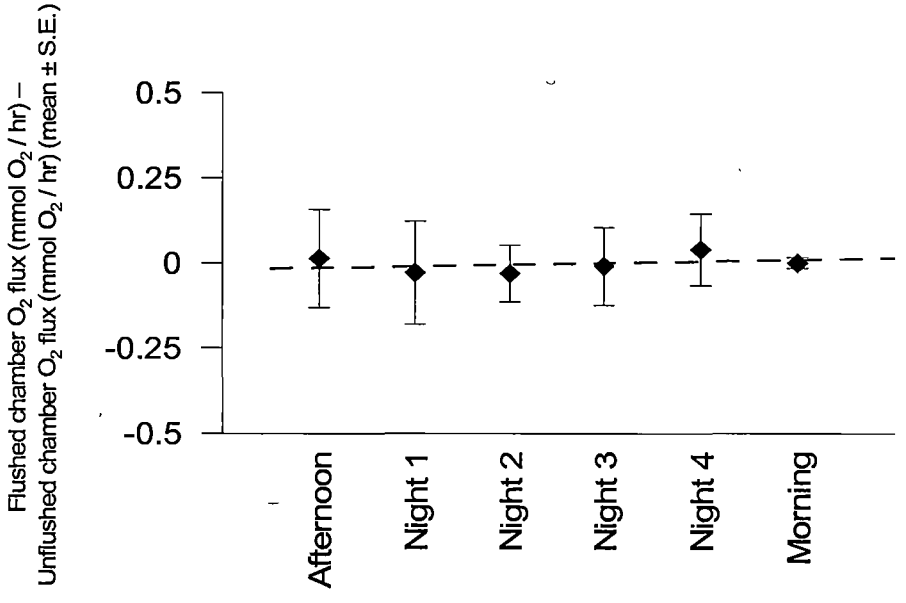

Figure 3.8. Net difference in flux estimates from paired flushed (every 4 hours) and unflushed chamber incubations (over 24 hours). Estimates are averages (± S.E.) from n=10 paired incubations across the different treatments included in the experiment. The sequence of 4 hour incubations between flushes enabled 1 afternoon (light), 4 night (dark) and 1 morning (light) comparisons. A linear regression fitted to the mean differences in flux estimates indicated that neither the gradient nor intercept differed significantly from zero (Regression: Slope, $T_{1,4}$ = 0.6579, P = 0.55^{ns}, intercept, $T_{1,4}$ = -0.7301, P = 0.51^{ns}).

3.5. DISCUSSION

Research into effects of NIS in marine habitats has largely been concerned with impacts on native species' populations and communities (e.g. Stewart & Haynes 1994, Creese et al. 1997, Crooks 1998a, Crooks & Khim 1999, Strayer et al. 1999b, Hedge & Kriwoken 2000, Schwindt et al. 2001). In contrast, the impacts of NIS on key ecosystem level processes, such as nutrient cycling and other aspects of the functioning of benthic communities has received far less attention. Ecosystem level effects are inferred from alterations to the native habitat and community structure. Quantifying changes to community function following the arrival of NIS may be particularly important if the invasive species is in some way an 'engineer' of habitat structure, given that ecosystem engineers are capable of drastically altering ecosystem processes determining carbon and nutrient cycling (Jones et al. 1994, 1997, Schwindt et al. 2001, Crooks 2002).

3.5.1 IMPACTS OF SCREWSHELLS ON COMMUNITY METABOLISM

Aggregations of screwshells at high densities, irrespective of whether they were alive, dead and empty or supporting hermit crabs, exhibited significantly higher gross primary production (GPP) than treatments with low densities of shells, and the controls. This reflects a higher primary producer biomass (PPB) in the high density treatments, stemming from a greater abundance of both sediment microphytobenthos (MPB) and epiphytic algae growing on the hard substratum of the screwshells. The presence of the screwshells, particularly at high densities, effectively forms a semi-consolidated matrix on the benthos, allowing the colonisation of the benthic habitat by filamentous algae. Where screwshells are

sparse there is a marked reduction in epiphytic filamentous algae, and filamentous algae were non-existent in the control plots. It is well recognised that the availability of hard substratum provides a surface for attachment of a variety of epibenthic sessile invertebrates and algae in many soft-sediment benthic ecosystems (Reise 2002, Callaway 2003, O'Brien et al. 2006), and clearly explains the positive correlation between higher densities of screwshells and higher biomasses of filamentous algae observed in this experiment.

Perhaps of more interest is the greater biomass of MPB associated with the sediment in plots with high densities of screwshells compared to the control plots. High densities of shells are likely to alter hydrodynamic processes at small scales (Eckman 1983, Crooks & Khim 1999), particularly at the benthos/water interface, reducing disturbance of the sediment. This is likely to facilitate MPB production, and may explain the increase in biomass observed. Alterations to very small scale hydrodynamic processes are regarded as important impacts (Crooks & Khim 1999, Lenihan 1999), and certainly sediment disturbance has been demonstrated as important in defining sediment MPB communities (Webb & Eyre 2004b). Screwshells are also capable of producing large quantities of pseudofaeces (Scott 1997, Bax et al. 2003, Gunasekera et al. 2005), which may not only act to consolidate sediments, but may also increase the biotic loading of the benthos (Ricciardi et al. 1997, Crooks & Khim 1999), increasing the release of dissolved nutrients that are required for MPB growth. The increase in MPB biomass may also be due to a shift in the composition of the microalga communities. Like the infauna, MPB assemblages are strongly influenced by sediment grain size. Given that

sediment grain size changed in the presence of screwshells at high densities (see chapter 2), this may also partially account for the change in the biomass of primary producers. Irrespective of the mechanism, higher densities of shells promote higher biomasses of primary producers (both MPB and epiphytes), which in turn leads to higher GPP.

High density accumulations of screwshells also exhibited significantly higher gross community respiration (GCR) than patches with fewer, or no, screwshells. However, unlike GPP, GCR differed depending upon whether screwshells were alive, dead or supporting hermit crabs. Within the high density treatments, rates of respiration in HL treatments were 33 % greater than in HD treatments, and 38 % greater than in HHC. The higher GCR in the accumulations of high densities of screwshells is likely to be due to the higher abundance and concomitant respiration of infauna and epifauna. The difference between the HL treatment and the HD and HHC treatments is likely to be a direct result of the significant oxygen demand of the live screwshells themselves. Increasing GCR with increasing mollusc biomass was also observed other mollusc species, such as *Crepidula fornicata* (Martin et al. 2007c) and *Atrina zelandica* (Gibbs et al. 2005) which both exhibit broadly similar ecological characteristics to *M. roseus* (i.e. suspension feeders). It is also likely that benthic bacterial respiration has been stimulated through the biodeposition of the screwshells, further contributing to the higher GCR in this treatment. Surface biodeposition is known to enhance oxygen consumption rates and potentially limit the penetration of oxygen into the benthos (Norling & Kautsky 2007).

The GCR in the HD and HHC treatments was significantly less that the HL treatment, but not significantly different from one another. There are a number of plausible explanations for this. Given that the major difference between HD and HHC treatments was that 50% of the shells in the HHC treatment were occupied by hermit crabs, the lack of a significant difference between HD and HHC treatments may indicate that the oxygen demand of hermit crabs is very low. Alternatively, the HHC treatment had a significantly lower biomass of polychaetes when compared to other treatments. Therefore, while the HHC treatment had a higher biomass of *P. tuberculatus*, the respiration associated with this species is potentially offset by the respiration from the much higher abundance of polychaetes in the HD treatment. This is certainly plausible, given that polychaetes constituted ~50% of the total biomass in the HD treatment plots, and are therefore highly likely to be a significant contributor to the GCR for that treatment.

In every treatment, including controls, net oxygen flux (estimated from GPP and GCR) was always negative, indicating that the site is net heterotrophic regardless of screwshell density and state. Because alterations to community function assessed in terms of DO (oxygen flux) provide a robust proxy of community function, and accurately reflect other estimates used in quantifying community metabolism (namely energy or carbon flow), Bligh Point can be considered as an energy and carbon sink. The benthos is utilising more oxygen (energy) through GCR than it produces via GPP, irrespective of the presence of screwshells, and whether shells are alive, dead or supporting hermit crabs. Therefore, all configurations of the benthos at this site require an influx of energy from adjacent benthos and/or from

the water column. However, areas of the benthos dominated by live screwshells are almost twice as demanding (double the net DO flux) than areas unoccupied by screwshells. This suggests that communities in areas occupied by live screwshells at high densities exhibit twice the energy requirements than benthic communities associated with bare sediment.

Another useful metric is the GPP:GCR ratio (Odum 1969), which is considered a direct estimate of community metabolism as it effectively integrates all changes in oxygen including production by all primary producers (MPB, filamentous algae and macroalgae) and their respiration, in addition to the respiration of infauna, epifauna and bacteria (Norling & Kautsky 2007). The fact that the GPP:GCR ratio from all treatments was < 1 again indicates that benthic communities in all of the different treatments require a net exogenous input of energy to sustain the current level of biomass productivity. Of particular interest was the fact that the HD and HHC treatments exhibited the highest GPP/GR ratios, significantly higher than live screwshells at the same density, and much higher than the lower density treatments and controls, indicating that the HD and HHC treatments require relatively less exogenous influx of energy for a given amount of production than the other treatments. This clearly indicates that metabolism and/or energy flow in areas dominated by screwshells is fundamentally governed not on density alone, but also whether screwshells are alive or not.

3.5.2 IMPLICATIONS OF FUTURE INVASIONS OF NEW HABITAT BY M. ROSEUS.

There is little doubt that where it has invaded Australian waters and established at high densities, *M. roseus* has greatly influenced the physical structure of the benthos and the relative abundance of native species (Chapter 2). It can be viewed as an ecosystem engineer in the true sense of the term. Further, the quantitative evidence from this study indicates that *M. roseus* drastically alters functional aspects of invaded habitats. Given that *M. roseus* has now become one of Australia's most widespread introduced marine species, occupying extensive areas of Australia's east coast across a wide variety of habitat types and depths (Allmon et al. 1994, Gunasekera et al. 2005), its overall impact on benthic community structure and function in soft-sediment environments out to the continental shelf is likely to be dramatic.

Of particular interest is that the impacts of *M. roseus* on community function differ across the different screwshell states. Generally, communities associated with high densities of live screwshells were far more energy demanding than benthic communities associated with high densities of dead and empty screwshells or screwshells containing hermit crabs, although the productivity of the different states was similar. This can essentially be attributed to the fact that screwshells themselves utilise extensive quantities of oxygen, but the production from MPB and epiphytic algae is the same irrespective of if screwshells are alive, dead or supporting populations of hermit crabs.

The different impact across the different screwshell states has potential implications because depending on the area, screwshell accumulations may consist primarily of live individuals (95 % alive), or mostly dead screwshells, and in some benthic habitats, the dead shells are almost totally occupied by hermit crabs. For example, in eastern Bass Strait, vast areas support aggregations of screwhells at high densities (1200 m^{-2}) most of which (99%) are dead and occupied (85 %) by hermit crabs. Separating the effects of screwshells in different 'states' enabled quantifying different facets of impact.

First, given the persistence of dead shells, and that effects on community structure and function exist when accumulations are dominated by dead shells, impacts are long-lasting and can build as dead shells accumulate. The persistence of *M. roseus* shells is very high; as they are thick-walled, resistant to predation and do not easily fragment, even in high energy surf zones. Further, the shell's longevity is also likely to be prolonged when utilized by hermit crabs, as the crabs retain the shell above the sediment surface where it is less likely to bio-erode (Hazlett 1981, Reiss et al. 2003).

Second, the impact of *M. roseus* on community metabolism is likely to vary across space and time, depending on the 'state' of screwshells within a given accumulation. Newly invaded communities, dominated by living screwshells at high densities will be highly energy demanding, requiring up to twice as much energy influx than areas without screwshells to support the community. Other areas of benthos which are dominated with accumulations of dead shells will be far less energy demanding. The

absence of living screwshells will markedly reduce the oxygen demand, but the high primary production associated with the high PPB attached to the hard substratum provided by the shells will be maintained.

The fact that the impacts of *M. roseus* on the function of native benthic communities are dependent not only on the density of the NIS, but also whether the shells are dead or alive is a potentially novel feature. Importantly, inferring impacts on the functioning of the community based solely on changes to community structure and/or the abundance of select species is likely to have led to different interpretations to those based on direct measurement of community metabolism. Clearly, quantitative assessment of alterations to community function inflicted by a NIS (particularly one which changes the physical structure of the recipient habitat) provides a more robust estimate of overall impact than an assessment focusing on community structure alone.

3.5.3 POTENTIAL ARTEFACTS

While the use of *in situ* metabolic chambers to quantify community metabolism is relatively new in assessing the impact of NIS, the practice has been used in both marine and freshwater systems to characterize the metabolic activities of native communities (e.g. Klumpp et al. 1987, Martin et al. 2007a, b). A concern in using this kind of equipment is that the incubated community may be negatively affected by declining oxygen concentrations within the chamber. However, given a highly linear pattern of oxygen decline, and that DO flux rates from chambers flushed

every 4 hours were identical to those of unflushed chambers deployed above the same community, I can be confident that the incubated community was not adversely affected by the incubation conditions.

Caging artefacts can potentially confound true treatment effects and therefore make interpretation of results difficult (Hulberg & Oliver 1980). However, there was no evidence that the presence of a PVC 'fence' around the perimeter of plots used to maintain treatment densities throughout the experiment had any influence on results as evident by no significant differences in any of the biotic or abiotic parameters measured between fenced and unfenced controls.

3.5.4 CONCLUSIONS

Maoricolpus roseus is an ecosystem engineer that is not only capable of modifying the physical structure of the habitat, but also the composition and functioning of the recipient community. Community function differed markedly, not only across different screwshells densities, but also across the different screwshell states (live shells, dead shells and dead shells supporting hermit crabs). Importantly, because *M. roseus* shells are capable of persisting in the environment for very long periods of time, particularly if they are occupied by hermit crabs, then the impacts associated with this ecosystem engineer will last well past the lifespan of living shells.

CHAPTER 4

IMPACTS OF NEW ZEALAND SCREWSHELLS (MAORICOLPUS ROSEUS) ON SCALLOP DISTRIBUTION AND BEHAVIOUR: A MULTI-SCALE APPROACH.

4.1. ABSTRACT

Introduction of the New Zealand screwshell, *Maoricolpus roseus*, to Tasmania and its subsequent invasion of vast areas of SE Australia has sparked concern over its potential impact on native soft-sediment assemblages and, in particular, on commercially harvested mollusc species. I quantify the impact of both live and dead and empty *M. roseus* shells on the distribution of two sympatric scallop species, queen scallop (*Equichlamys bifrons*) and doughboy scallop (*Chlamys asperrimus*) which are both harvested in a recreational fishery. I also quantify the impact of *M. roseus* on the distribution and behavior of the commercial scallop (*Pecten fumatus*) which are harvested both commercially and recreationally in Tasmania. I relate the distribution of *M. roseus* to that of all three scallop species at large spatial scales, and quantify impacts of the screwshell on the distribution and behavior of *P. fumatus* at small spatial scales using surveys and *in situ* experiments. Across large spatial scales (1-50 km), the highest densities of all three scallops were observed at the lowest screwshell densities, and in areas with low silt content in the benthic sediments. Both *E. bifrons* and *C. asperrimus* were also observed at high screwshell

densities, albeit in low numbers, but no commercial scallops were ever observed at screwshell densities greater than 200 m^{-2}. Additionally, all three scallop species showed size-specific (and therefore age-specific) patterns of distribution with increasing screwshell density, with only adult scallops observed to co-occur with high densities of screwshells. Small scale distributional patterns were also assessed for *P. fumatus*. Habitat selection by *P. fumatus* appears to occur at the scale of ~0.1 m. Adult *P. fumatus* were never observed atop dense mats of screwshells, but were instead observed recessing into small patches (e.g. 0.25 m^2 in area) of bare sediment unoccupied by screwshells. In experiments when offering a choice between screwshell mats and bare sediment, *P. fumatus* actively selected bare areas of the benthos in which to reside. The survey and experimental results yielded evidence of avoidance of benthic habitat dominated by high densities of screwshells. Although all three scallop species showed evidence of preference for bare sediment, the pattern of avoidance of screwshells was most clearly evident in the distribution and behavior of *P. fumatus*. Given the wide-spread distribution of *M. roseus* at high densities across large areas the continental shelf in SE Australia, impacts of this species on scallop distribution and behavior have the potential to greatly affect both commercial and recreational scallop fisheries in the region.

4.2. INTRODUCTION

The invasion of new areas by non-indigenous species (NIS) is considered one of the greatest ecological threats in both terrestrial and aquatic systems worldwide. In marine realms alone, human-mediated introductions have been documented to drastically alter both the structure and functioning of recipient habitats and their associated communities (Carlton et al. 1990, Carlton & Geller 1993, Carlton 1996b, a, Cohen & Carlton 1998, Ruiz et al. 1999, Ruiz et al. 2000, Crooks 2002, Ross et al. 2002, 2003b, a, Ruiz & Hines 2004). Further, NIS are estimated to cost millions of dollars annually, both in biosecurity measures to prevent arrivals and in implementing management responses to those already established. However, funds and other resources allocated to tackling issues arising from NIS are limited and therefore NIS must be prioritized for management actions based on their imminent and potential impact to native assemblages and habitats (Byers 2002b, Ross et al. 2002, 2003b).

NIS of particular concern include those which have the potential to impact profoundly on commercially important species (Halary et al. 1994, Mann & Harding 2000, Talman & Keough 2001, Ross et al. 2002, Knowler 2005). Documented impacts of marine NIS include predation on native species (Mann & Harding 2000, Ross et al. 2002, Knowler 2005, Rilov 2009), competitive interactions between native and invasive species for habitat and food resources (Talman & Keough 2001, Thieltges 2005, Byers 2009), and alterations to native species abundances through modification to the 3-dimensional complexity of the benthic habitat (Crooks &

Khim 1999, Lenihan et al. 2001) and modifications to the flow of energy through native food webs (see review by Grosholz & Ruiz 2009).

Molluscs in particular have been successful invaders of marine habitats, many of which have negatively impacted commercially important native species (Mann & Harding 2000, Talman & Keough 2001, Thieltges 2005). A most successful mollusc invader of Australian waters is the New Zealand screwshell (*Maoricolpus roseus*), a turritellid gastropod inadvertently introduced during the 1920s. Since its arrival, *M. roseus* has become one of Australia's most widespread marine NIS and now occupies a variety of soft-sediment and hard substratum habitats from southern Tasmania to northern New South Wales (Allmon et al. 1994, Gunasekera et al. 2005, Nicastro et al. 2009). *M. roseus* regularly attains densities of 600 - 1200 m^{-2} (Allmon et al., 1994), and up to 2500 m^{-2} (Reid, 2003). The ability of *M. roseus* to dominate benthic habitats at very high densities is of particular concern, as a number of commercially important species occupy similar habitats and exhibit similar ecological characteristics (e.g. filter feeding) to that of the screwshell.

The native species of greatest concern is the commercial scallop, *Pecten fumatus* (Reeve 1852). Anecdotally, *P. fumatus* and *M. roseus* appear to exhibit almost identical habitat preferences, both occupying a range of substratum types from mud to coarse sand, and tend to prefer areas of moderate to strong benthic currents. Moreover, both species are ciliary suspension feeders and therefore do not only use the same mechanisms for food capture, but possibly utilize similar food resources. While direct competition for food resources is likely to be a potential mechanism of

impact (see Chapter 5), the strong overlap in habitat preferences of both species also suggests the potential for screwshells to affect the distribution and behavior of *P. fumatus* through occupying its usual habitat.

In this chapter I quantify the level of overlap in habitat use between *M. roseus* and three sympatric scallop species (including *P. fumatus*) at both large ($5x10^1$ m) and small (10^{-1} mm) scales using a variety of survey techniques. I then complement patterns observed in the surveys with small scale *in situ* manipulative experiments to examine the mechanisms of impact, which help to explain patterns observed in the surveys.

4.3. METHODS

4.3.1 LARGE-SCALE DISTRIBUTIONAL PATTERNS OF SCREWSHELLS AND SCALLOPS

The D'Entrecasteaux Channel is a narrow stretch of water separating Bruny Island from the southeast coast of mainland Tasmania (Figure 4.1). It extends approximately 55 km, between the estuaries of the Huon River in the south and the Derwent River in the north. While the central passage of the channel is dominated by narrow sections exhibiting high current flows, course-grained substrata and small areas of patchily distributed rocky reef, the D'Entrecasteaux Channel also branches into a number of embayments with low velocity currents and accumulated fine sediments. The D'Entrecasteaux Channel supports a wide diversity of marine flora and fauna, including extensive beds of commercial scallops (*Pecten fumatus*) and introduced New Zealand screwshells (*Maoricolpus roseus*), in addition to small beds of queen scallops (*Equichlamys bifrons*) and doughboy scallops (*Chlamys asperrimus*). A total of 20 sampling locations were selected, spanning the length of the D'Entrecasteaux Channel, encompassing sedimentary habitats ranging from coarse-grained substrata to fine silts.

At each location, scallops and screwshells were counted within 1 m either side of a 50 m transect line. Although the primary scallop species of interest was *Pecten fumatus*, because it is the target of a recreational and commercial fishery in Tasmania, the two other scallop species were also enumerated since their distribution may influence that of *P. fumatus*. The transect was divided into 2 m lengths, enabling density estimates of screwshells and scallops to a spatial resolution of 2 m x 1 m sections. A SCUBA diver sampled each 2 x 1 m section on either side

of the transect line. Within each 2 x 1 m section, screwshells were counted and scallops identified to species, counted and the shell width (the same standard measure used by the commercial and recreational fisheries) measured. Screwshell dimensions were not measured. The sediment type in each 2 x 1 m section was also scored qualitatively from coarse sand through to fine silt (on a scale of 0-5) on the basis of sediment size and the quantity of shell grit.

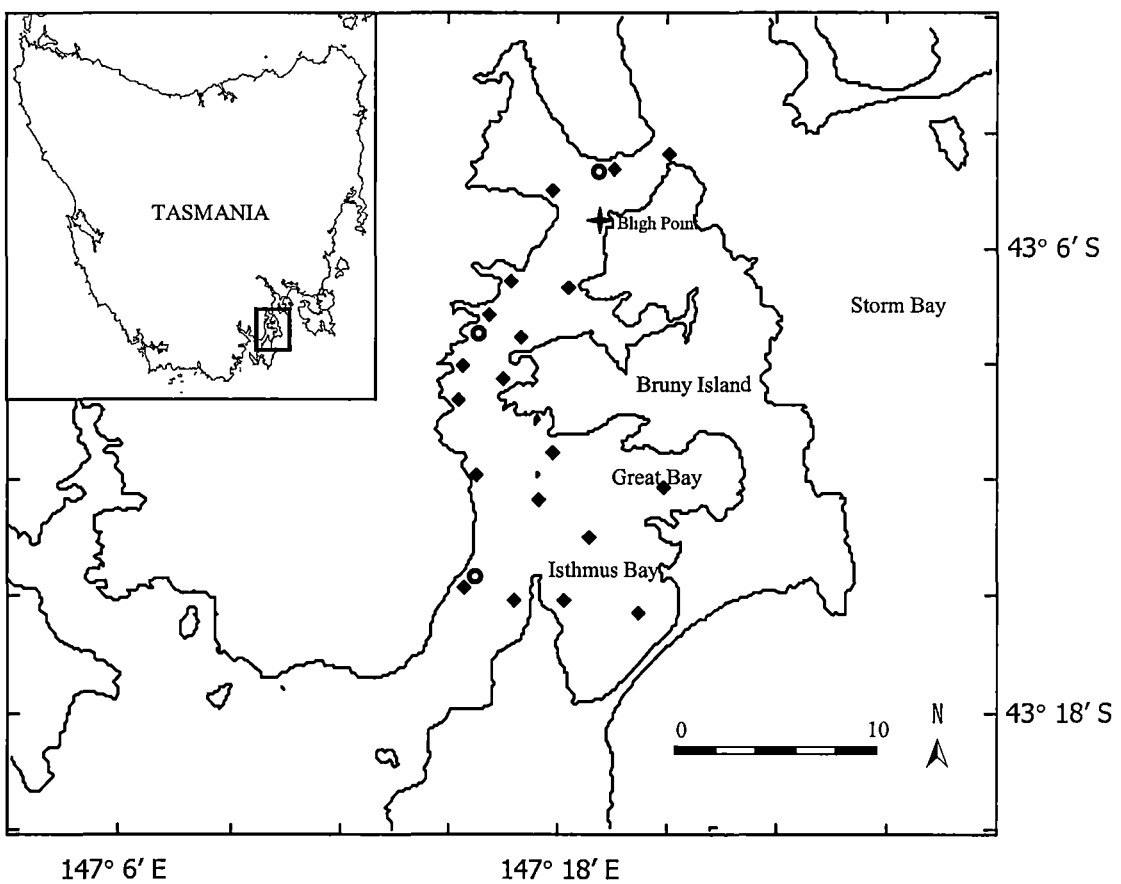

Figure 4.1. Map of the D'Entrecasteaux Channel, Tasmania, showing the locations of large scale transects for all 3 scallop species (◆), small scale surveys conducted for *P. fumatus* (●), and the *in situ* behavioral experiments conducted using *P. fumatus* (✦).

4.3.2 SMALL-SCALE DISTRIBUTION OF SCREWSHELLS AND COMMERCIAL SCALLOPS

Because results from the large scale survey indicated that *Pecten fumatus* was the most abundant of the scallop species, further surveys at smaller scales were devised to examine the relationship between screwshells and this species. The small-scale surveys were conducted at three sites, using an elongated quadrat consisting of ten 100 x 100 mm steel squares welded together in line to form a 1 m long strip of 100 mm^{-2} mesh. On locating a commercial scallop, one end of the quadrat was placed adjacent to the scallop, pointing in a direction derived from random compass bearing. A second quadrat was then placed perpendicular to the first, a third perpendicular to the second and a fourth perpendicular to the third. When all 4 quadrats were placed around the scallop, a 'cross-hair' was formed with quadrats 1 and 3, and 2 and 4, opposing one another respectively, with the scallop in the centre (Figure 4.2). The number of screwshells in each 100 mm^{-2} section was then counted and recorded to estimate density of screwshells at different distances from the scallop. The number of screwshells in the 100 mm^{-2} directly beneath the scallop was also counted. Finally, the shell width of the scallop was measured.

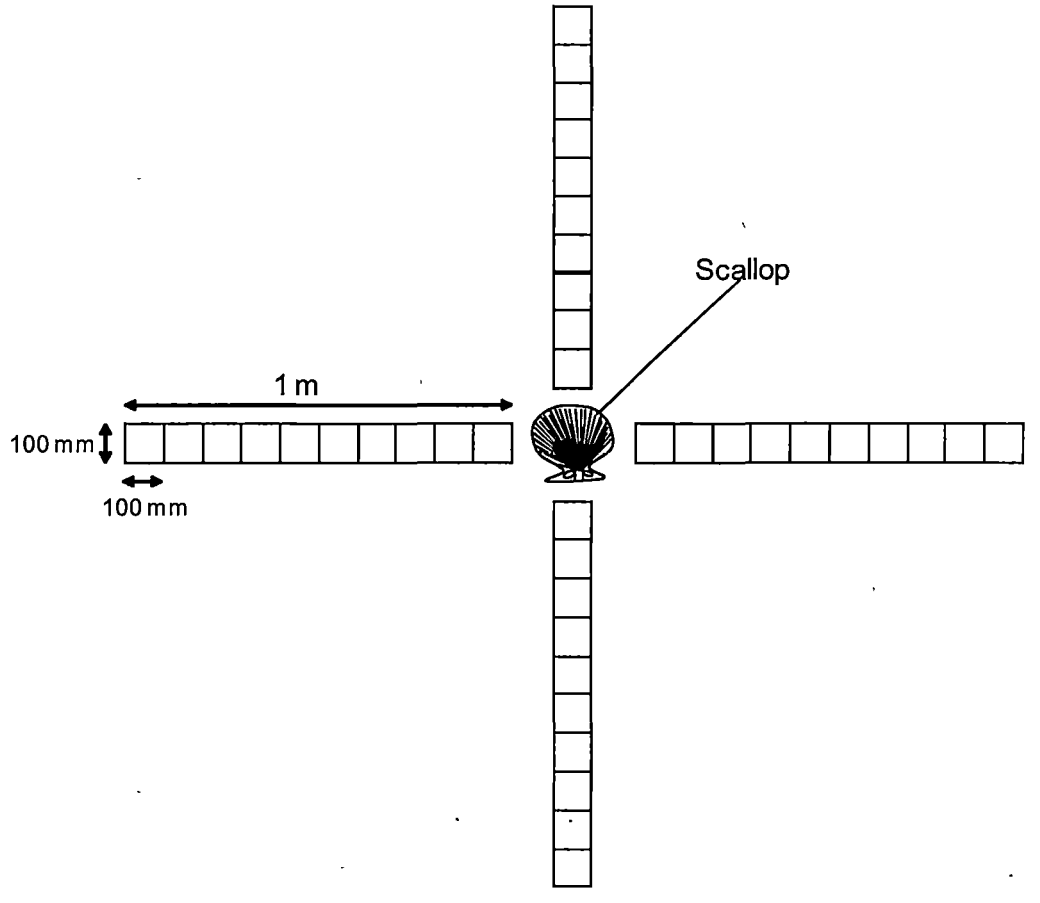

Figure 4.2. The 'cross-hair' alignment of 4 elongated quadrats in relation to a scallop. Screwshells were counted and photographed in each of the 100 by 100 mm sections of each quadrat.

4.3.3 IN SITU MANIPULATIVE EXPERIMENTS

To complement the patterns observed in the large and small scale surveys, an *in situ* caging experiment was used to quantify small scale patterns in habitat selection. Cages consisted of a rigid 60 mm high polyvinylcarbonate (PVC) ring (1 m^2) attached to a ring of oyster mesh (600 mm high, mesh size of 20 x 20 mm). Cages had no roofs or floors. Attached to the top of the cages was a small curtain of soft mesh supported by buoys to prevent sea stars (potential predators) entering the

cages. Pilot trials indicated that sea stars were unable to enter the cages, and that cage walls were sufficiently high to prevent scallops from escaping. Cages were pushed into the sediment to a depth of 80 mm and held in place by metal star pickets driven into the sediment.

Dead and empty screwshells added at a density of 1200 m^{-2} to one half of the cage and the second half of the cage was left bare. The half of the cage containing screwshells formed a complete carpet of shells, with no patches of bare substratum. Screwshells were added 1 week before the scallops. Adult *P. fumatus* (80-100 mm) were then allocated randomly to either the bare substratum, or the 'screwshell half' of each cage, initially using only a single scallop per cage. A second and third trial was then conducted using higher scallop densities of 2 scallops and 4 scallops per cage respectively, again allocating all scallops to one half of the cage (either bare substratum or the screwshell bed) at random. A total of 16 replicate cages were deployed in each trial.

4.3.4 STATISTICAL ANALYSES

The relationship between scallop density and screwshell density from the large scale transects was assessed individually for each of the three scallop species. Initially, relationships were assessed at the transect scale, using data averaged across all 2 m^{-2} sections within each transect. The relationship at a scale of each 2 m^{-2} section was then assessed independently. In these analyses, a zero-inflated Poisson model was fitted to explain the relationship between *P. fumatus* density and screwshell density. For *E. bifrons* and *C. asperrimus*, given large numbers of zero counts (absences of

scallops), the data for these species were transformed into a binomial response (present/absent) and a log-binomial model fitted, with the screwshell density being the single predictor included in the model. This enabled an estimation of the change in the likelihood of finding a scallop with increasing screwshell density, through the interpretation of risk ratios.

For the small-scale 'cross-hair' surveys carried out using only *P. fumatus*, linear regressions were fitted to relationships between screwshell density and increasing distance away from a given *P. fumatus* individual. Individual regressions were fitted for each of the three sites used in the survey. Log binomial and regression analyses were conducted using SAS version 9.1 (Cary, NC, USA). Data obtained from the *in situ* manipulative experiment were assessed using replicated G-tests with scallop density as a factor (after Sokal & Rohlf 1995).

4.4. RESULTS

4.4.1. LARGE-SCALE DISTRIBUTIONAL PATTERNS OF SCREWSHELLS AND SCALLOPS

Of the three scallop species, the strongest distributional patterns were observed for *P. fumatus*. *Maoricolpus roseus* and *P. fumatus* co-occurred at all 20 survey sites sampled within the D'Entrecasteaux Channel, albeit at vastly different densities. The maximum density was 1952 m^{-2} and 5 m^{-2} for *M. roseus* and *P. fumatus* respectively. The abundance of screwshells was notably higher in the northern and southern most survey locations, with high densities of screwshells correlating strongly with coarse sediment types, dominated by sand and shell grit. *Pecten fumatus* was abundant throughout the D'Entrecasteaux Channel, although the highest densities of scallops were more prevalent in areas with low densities of screwshells (Fig 4.3).

Queen scallops (*Equichlamys bifrons*) were only observed at five survey locations, predominately in the southern half of the D'Entrecasteaux Channel. They tended to inhabit areas dominated by coarser sediment types, and in areas supporting low to moderate densities of screwshells (Fig 4.3). Doughboy scallops (*Chlamys asperrimus*) were found at 8 of the 20 sites, also only in the southern half of the D'Entrecasteaux Channel. The highest densities of *C. asperrimus* were also associated with coarse sediment types. All three scallops tended to avoid silty and muddy sediments and inhabit areas dominated by coarse-grained sediments.

Based on average densities per transect (scales of 100 m^{-2}), the density of all three scallop species showed a negative relationship with increasing screwshell density, in

that even low densities of scallops were never observed in areas occupied by screwshells at moderate densities (e.g. ~ 600 m^{-2}) (Fig 4.4).

Evidence of a negative relationship between scallop and screwshell density was more clearly evident at the scale of 2 m^{-2} where densities of *P. fumatus* declined significantly with *M. roseus* density (Fig 4.5). Benthic habitats occupied by even low to moderate screwshell densities supported few, if any, *P. fumatus* individuals (Fig 4.5). At this scale, once screwshells densities attained 200 m^{-2}, no *P. fumatus* individuals were observed. Note that all *P. fumatus* individuals identified in these surveys were partially buried in the sediment, and at no stage were any scallops observed atop mats of screwshells.

On the few transects where they occurred, both *E. bifrons* and *C. asperrimus* showed similar results to that of *P. fumatus*, with the highest densities associated with the lowest densities of screwshells. Unlike *P. fumatus*, *E. bifrons* was still observed at screwshell densities of ~ 1600 m^{-2} and *C. asperrimus* was observed among screwshells at ~ 300 m^{-2} on one occasion (Fig 4.5). This indicated that both *E. bifrons* and *C. asperrimus* were capable of inhabiting areas of benthos that also supported moderate-high densities of screwshells, which was clearly not the case for *P. fumatus*. Further, whilst *P. fumatus* was only ever found recessed into the sediments, this was much less common for *E. bifrons,* and never observed for *C. asperrimus*. Both *E. bifrons* and *C. asperrimus* were regularly observed atop dense beds of screwshells, and on several occasions *C. asperrimus* was physically attached via byssus threads to *M. roseus* shells.

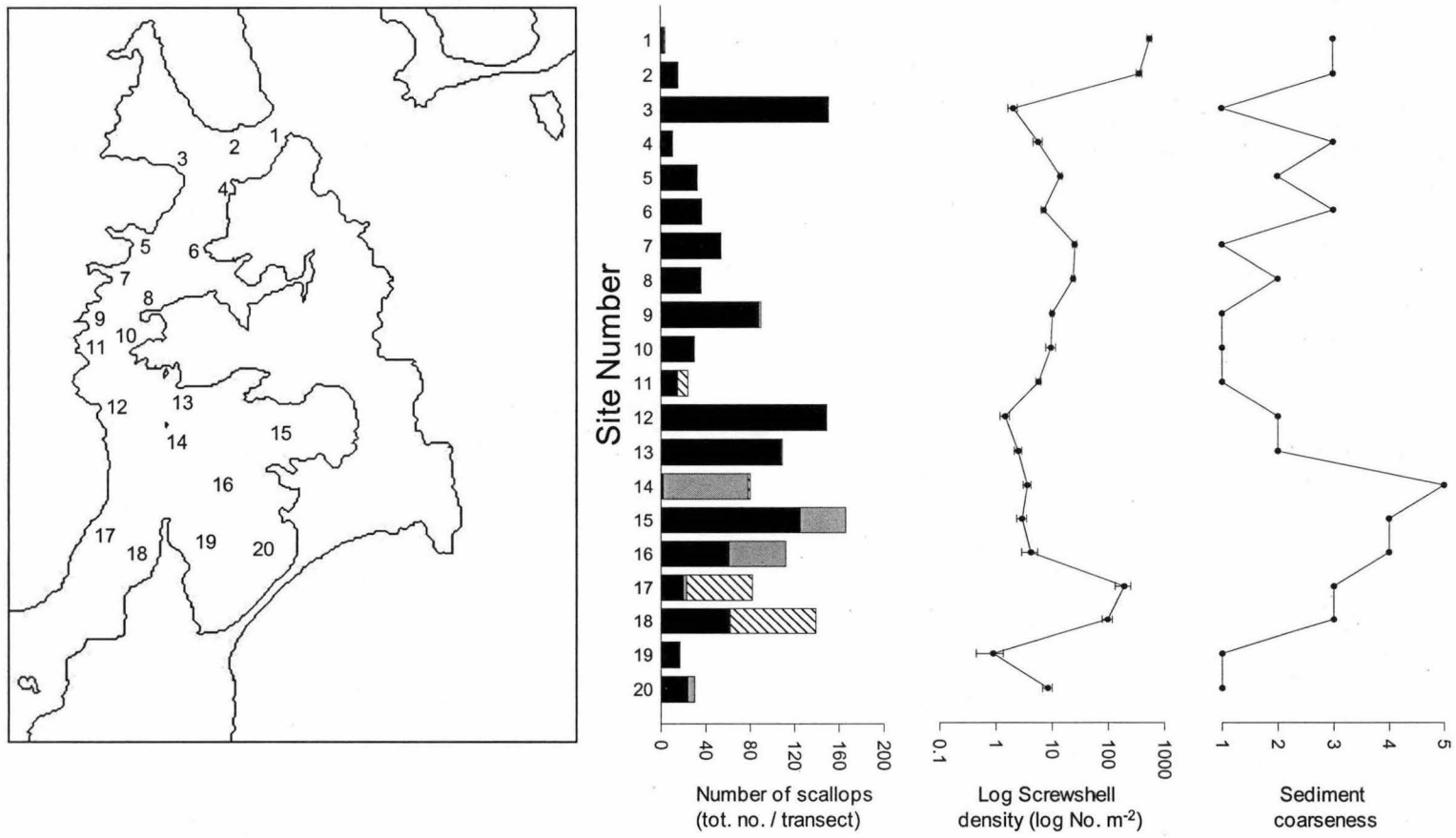

Figure 4.3. The distribution and total number of *Pecten fumatus* (solid bars), *Equichlamys bifrons* (grey bars) and *Chlamys asperrimus* (hatched bars), screwshell density and qualitative sediment coarseness scores across the 20 sampling locations in the D'Entrecasteaux Channel. Screwshell density is represented as the average (± S.E.) of all 50 2 m^{-2} sections of each transect. Sediment coarseness was assessed qualitatively and recorded by the diver *in situ*.

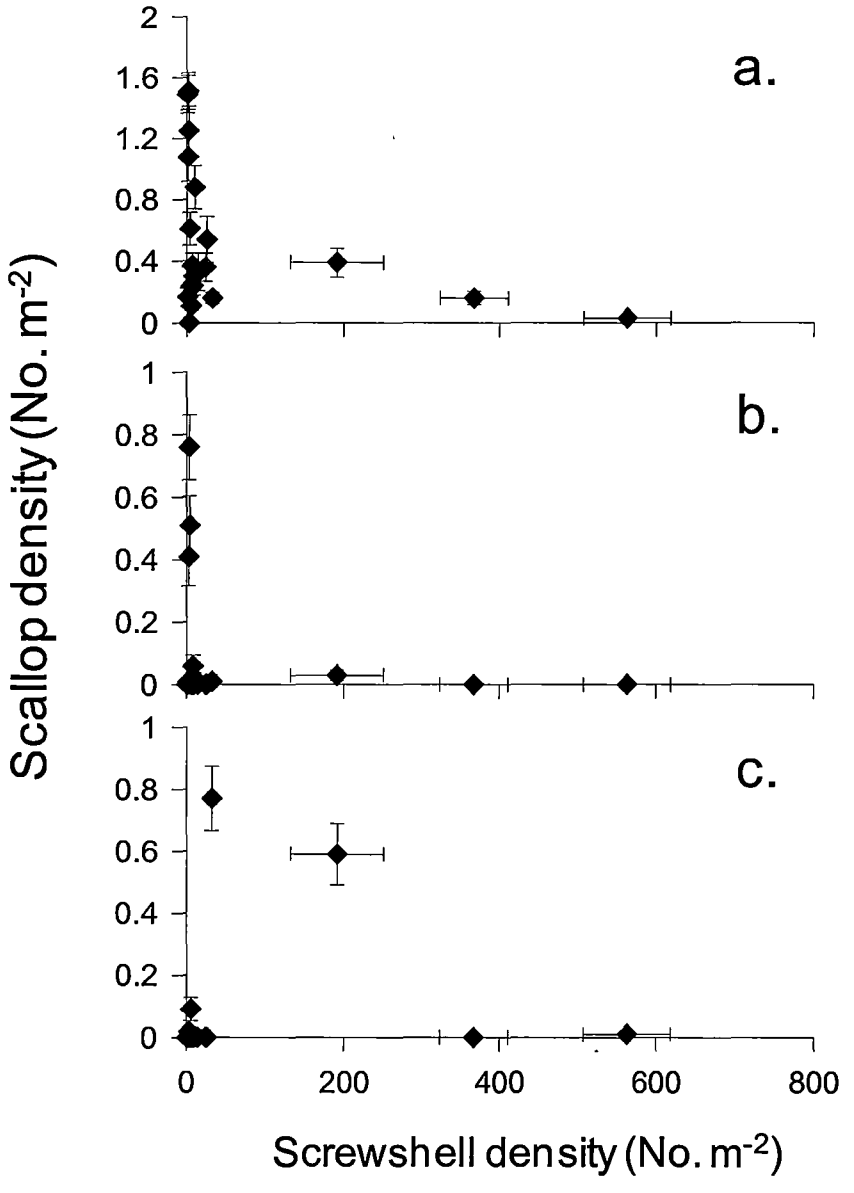

Figure 4.4. The relationship between *Pecten fumatus* (a), *Chlamys asperrimus* (b) and *Equichlamys bifrons* (c) and screwshell density for data averaged for each transect.

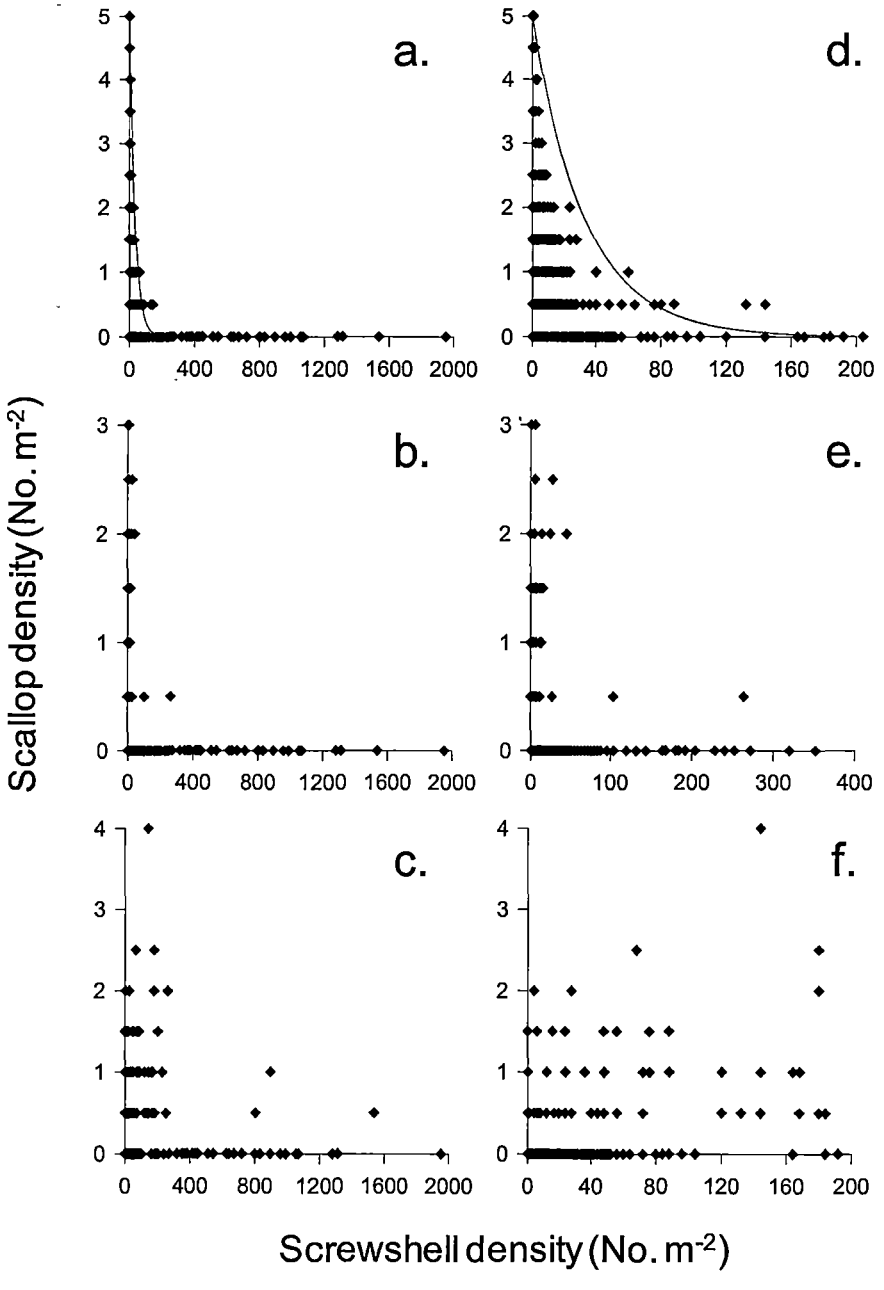

Figure 4.5. The relationships between *Pecten fumatus* (a, d), *Chlamys asperrimus* (b, e) and *Equichlamys bifrons* (c, f) and screwshell density. The figure has been divided into two sides, the left showing all data across all observed screwshell densities (up to 2000 m^{-2}), while the right hand side only shows the relationship up to a screwshell density of 200 m^{-2} (x-axis restricted to 200). The 95 % CI from the zero-inflated Poisson model are depicted for *P. fumatus*. Risk ratios derived from fitting log binomial models were r = 0.988 (95% CI 0.976, 0.999), P = 0.045 for *C. asperrimus*; and r = 1.001 (95% CI 1.001, 1.002), P = <0.001 for *E. bifrons*.

The zero-inflated Poisson model indicated a significant negative relationship between *P. fumatus* and screwshell density ($df = 1$, $T = -5.64$, $P<0.0001$) and that the density of *P. fumatus* decreased by 1.4 % for every unit increase in the density of screwshells. Risk ratios obtained from fitting a log binomial model species indicated that the probability of finding a scallop significantly decreased for *C. asperrimus* but increased for *E. bifrons*. The ratios indicated that for every increase of single screwshells, the likelihood of finding a scallop decrease by 1.2 % *C. asperrimus* and increase by 1.3 % for *E. bifrons*. I acknowledge that given the small number of observations for *C. asperrimus* and *E. bifrons*, the risk ratios for these species should be interpreted with caution.

Patterns of habitat occupancy by *Pecten fumatus* individuals were size specific. Juvenile scallops (<30 mm shell width) were located only at 3 sampling sites, which were those supporting the lowest densities of screwshells, and a moderately coarse sediment. Adult scallops were less specific in their choice of habitat, occupying habitats from fine silts though to coarse sands, and they often occupied habitats with moderate densities of screwshells. No juvenile *P. fumatus* were observed in habitats where screwshell density exceeded 15 m^{-2} (Fig 4.6). This trend was also evident among *E. bifrons* and *C. asperrimus*, although too few juveniles (<30 mm shell width) of these species were identified to suggest that the pattern is robust.

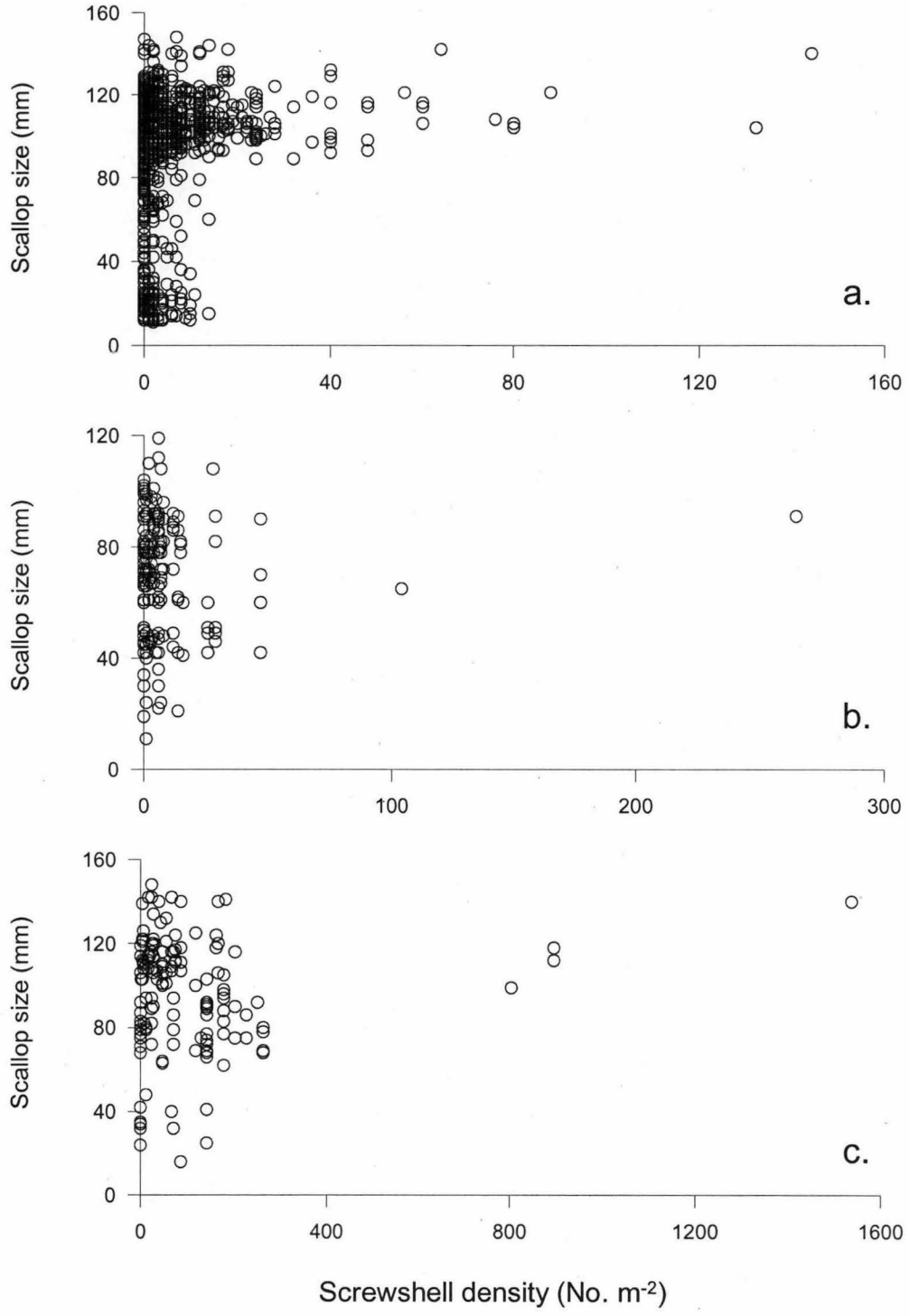

Figure 4.6. The relationship between different sized *Pecten fumatus* (a), *Chlamys asperrimus* (b) and *Equichlamys bifrons* (c) and screwshell density.

4.4.2 SMALL-SCALE DISTRIBUTION OF SCREWSHELLS AND COMMERCIAL SCALLOPS

In habitats where screwshells and commercial scallops co-occurred, specific habitat selection appeared to be occurring at a scale of ~ 10^{-1} m. Adult scallops were never observed atop dense mats of screwshells, but were invariably observed partially buried in small patches of bare sediment unoccupied by screwshells. These 'micro-depressions' were no larger than 0.25 m^2 in area. The density of screwshells increased with distance from a scallop occupying one of these 'micro-depressions' (Fig 4.7).

In the *in situ* caging experiment in which *P. fumatus* was offered the choice between bare substrata and screwshell 'mats' of equal area, individuals occupied the bare substratum significantly more often than the screwshell mats (Fig 4.8). Across the three *in situ* trials, 112 *P. fumatus* individuals were deployed (16 in the single scallop trial, 32 in the two scallop trial and 64 in the four scallop trial). A consistent pattern across all trials is that, of all scallops placed initially on bare substrata, not a single individual was observed to occupy the screwshell mat at the end of the experiment (Fig 4.8). A total of 7 scallops, across the 3 trials, were observed occupying screwshell mats at the conclusion of the experiment, although all of these scallops were initially deployed on to screwshells to begin with. The majority (89%) of scallops initially deployed on screwshell mats had moved to occupy bare sediment by the conclusion of trials.

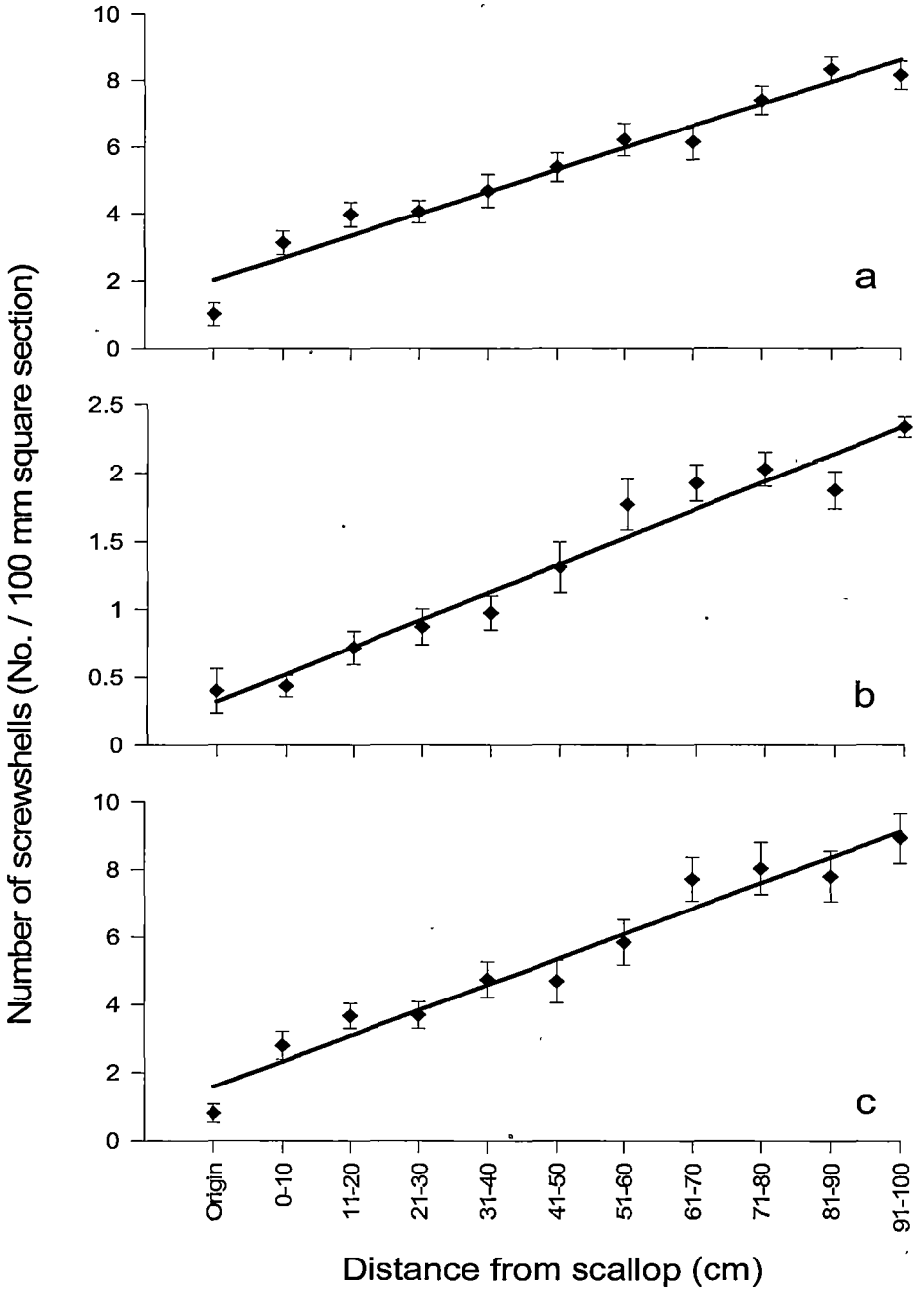

Figure 4.7. The relationship between screwshell density and proximity to a *Pecten fumatus* individual, derived from small scale 'cross-hair' surveys at three locations in the D'Entrecasteaux Channel. The three locations were the Northern Channel (a), Mid Channel (b) and Southern Channel (c). All three trends were derived from *n=10* scallops at each location. The relationship at all three locations exhibited positive linear slopes (Regressions: (a) Northern Channel: $y = 0.6564x + 1.3641$, $R^2 = 0.95$, $F_{1,9}=188.93$, $P=2.7 \times 10^{-7}$; (b) Middle Channel: $y = 0.2021x + 0.1175$, $R^2 = 0.95$, $F_{1,9}=190.85$, P=2.3 x 10-7; and (c) Lower Channel: $y = 0.7531x + 0.8172$ $R^2 = 0.9545$, $F_{1,9}=188.93$, $P=2.4 \times 10^{-7}$).

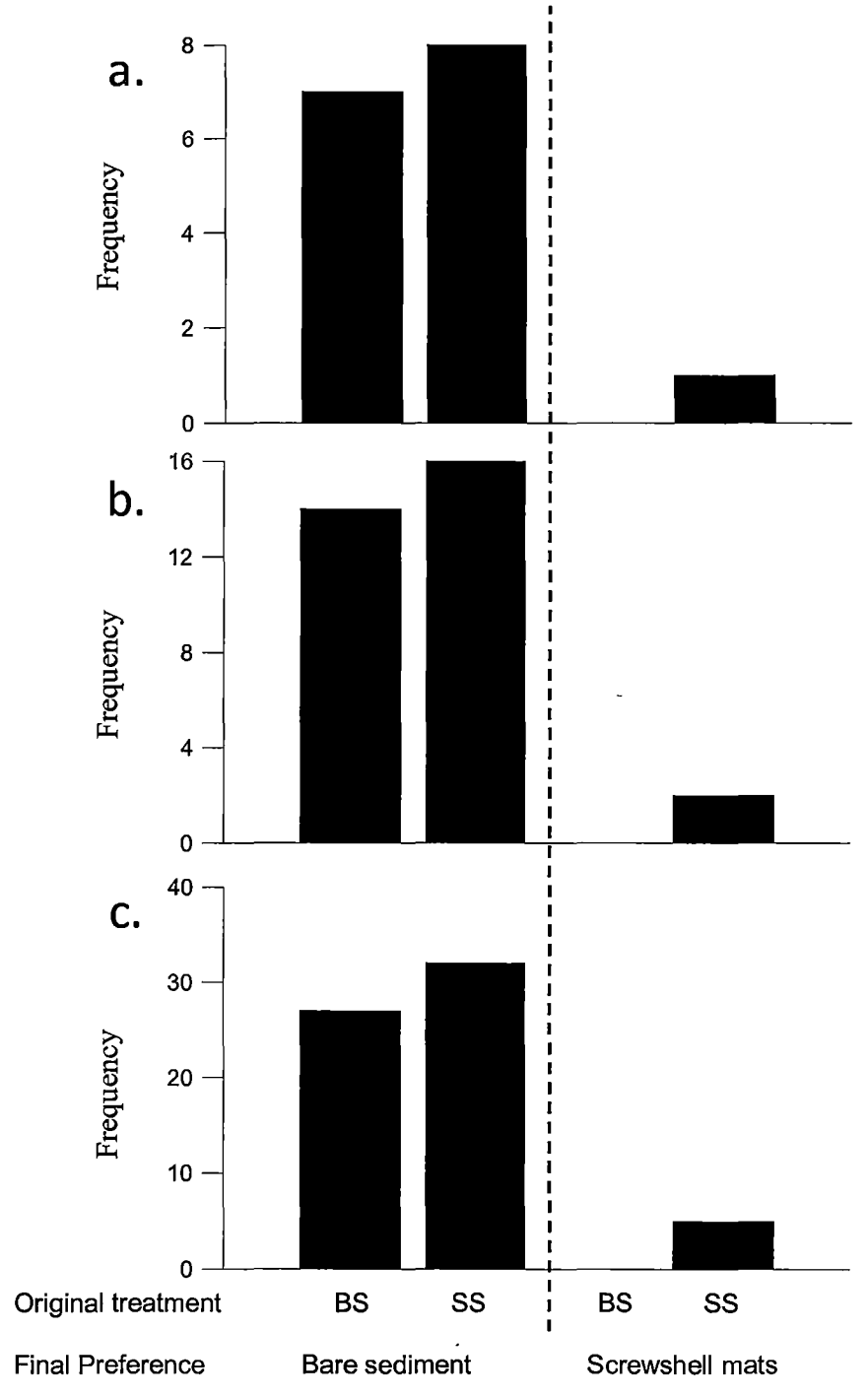

Figure 4.8. Results from the *in situ* manipulative experiment using a) single b) two and c) four *P. fumatus* adults per replicate cage. Original treatment refers to the initial substrata in which all scallops were placed within each cage; bare sediment (BS) or screwshell mats (SS). Final preference indicates the preferred substratum type occupied by the *P. fumatus* individuals at the completion of the experiment (Replicated G-Test: Test for homogeneity across scallop densities: $G = 0.62$, $df = 2$, $P = 0.73$, G-test for observed preferences $G = 360.49$, $df = 1$, $P < 0.001$).

4.5. DISCUSSION

4.5.1 DISTRIBUTIONAL PATTERNS OF SCREWSHELLS AND SCALLOPS

Correlating the spatial distribution of commercially important species with particular habitat characteristics and/or the distribution of potential predators and competitors may provide evidence of niche partitioning and help to elucidate mechanisms behind preferences of different species for particular habitats. At large spatial scales we assessed the distribution of the three scallop species, the substratum type and the distribution and density of *M. roseus*. Of the three scallop species, the strongest negative relationship with the distribution of *M. roseus* was exhibited by the commercial scallop (*Pecten fumatus*). Negative associations in the distribution of native species and NIS are a common phenomenon. Several studies of commercial scallop species in particular have reported findings analogous to those of this study, in which the distribution and density of the scallop is negatively associated with the distribution of both and native non-indigenous predators and competitors (Stokesbury & Himmelman 1995, Grall et al. 1996, Bologna & Heck 1999, Shumway & Parsons 2006).

The other scallop species in our study, *Equichlamys bifrons* and *Chlamys asperrimus*, exhibited only weak negative relationships with screwshells. While the highest densities of these scallop species were found in areas supporting the lowest densities of screwshells. Nonetheless, *E.bifrons* were still present at high screwshell densities (~1500m^{-2}), and some *C. asperrimus* individuals were also observed attached via byssus threads to *M. roseus* shells. The differences in distribution between the scallop species can in part be explained by ecological and biological

differences between the species. Unlike *P. fumatus* and *Equichlamys bifrons, C. asperrimus* is a sessile species which remains attached to the substratum throughout its life via byssus threads. In this case, *M. roseus* may represent a positive effect in providing an attachment substratum. In contrast, *E. bifrons* and *P. fumatus* are both free swimming species as adults. *Pecten fumatus* is usually partially buried in saucer-shaped depressions it creates in the sediment, while *E. bifrons* is often exposed atop the sediment surface, with the upper valve typically supporting a dense cover of filamentous algae and epibionts.

Avoidance of screwshells by *P. fumatus* was also evident at small spatial scales, where *P. fumatus* individuals were only observed in small patches of bare sediment that were inter-dispersed between screwshell accumulations. Selection for particular microhabitats has been extensively researched for a variety of marine species, and for scallops (Wolf 1993, Stokesbury & Himmelman 1995, Hunt et al. 2003, Greenawalt et al. 2004, Kamenos et al. 2004a, c, b). The consensus of this body of work is that scallops tend to preferentially occupy coarser sediment types over silt/muddy substrata. Moreover, many scallop species preferentially select complex 3-D habitats such as seagrass beds and sponge gardens in which to reside, which is perceived as a mechanism to minimise predation pressure (Shumway & Parsons 2006 and references therein). Given this, it was interesting to note that while *P. fumatus* and *E. bifrons* are free swimming species and occupy similar habitats at scales of 100 m^{-2} they utilize the same microhabitat in different ways. As previously mentioned *P. fumatus* is commonly partially in saucer-shaped depressions it creates in the sediment, while *E. bifrons* is often exposed atop the sediment surface, with the upper valve often supporting a dense cover of filamentous algae and epibionts.

This observation could be partially explained by the different species employing different strategies to avoid predation. Previous research has indicated that recessing behaviour is a mechanism used by a number of scallop species to avoid detection from predators (Shumway & Parsons 2006), and is certainly a potential predation-avoidance mechanism employed by *P. fumatus*. Alternatively, *Equichlamys bifrons* may be afforded some protection from predation by inhabiting areas of sediment also occupied by screwshells. Other studies have revealed that predation of scallops was lower in habitats with complex 3-D structures, such as is developed by growth of sponges, mussels and ascidians (Talman et al. 2004). Wolf (1993) indicated that *E. bifrons* preferentially occupied sea grass habitat over bare substratum, which was interpreted as a predator-avoidance mechanism afforded by occupying habitat with heighted 3-D complexity. Thus, the different utilisation of the habitat by *P. fumatus* and *E. bifrons* in the same locality could be explained, at least in part, by differences in predation-avoidance mechanisms employed by the different species.

4.5.2 MECHANISMS OF IMPACT ON PECTEN FUMATUS

Previous research has identified a variety of mechanisms which affect the distribution of scallop species at large spatial scales, namely larval supply, settlement, post-settlement recruitment (Shumway & Parsons 2006) may all play a role. At smaller spatial scales, competitive interactions for food resources have been also forwarded as a mechanism explaining the distribution of bivalve species (Peterson & Black 1987, 1988, Peterson & Beal 1989, Rheault & Rice 1996), including scallops (Pilditch & Grant 1999a, b). However, because *P. fumatus*

showed a preference for bare substrata over screwshell accumulations that consisted of only dead and empty shells, the lack of *P. fumatus* in areas with moderate-high densities of screwshells cannot be explained solely on the basis of competition with screwshells for food resources.

The most parsimonious explanation of the observed patterns is simply preference for a sedimentary substratum in which *P. fumatus* is able to partially bury (recess). Screwshells forming a dense 'mat' over the benthos prevents access of *P. fumatus* to bare sediment for potential burial, i.e. scallops are unable to recess. Previous research has attributed recessing behavior as a mechanism to optimize feeding currents (Kirby-Smith 1972, Wildish et al. 1987, Wildish & Kristmanson 1988, Wildish & Saulnier 1992, 1993, Pilditch & Grant 1999b), minimize predation (Shumway & Parsons 2006) and/or potentially assist in expulsion of pseudo-faeces and waste products. Thus in areas where screwshells 'mat' the benthos, scallops unable to recess on top of screwshell 'mats' may have to deal with sub-optimal current speeds, turbulence and other atypical boundary layer conditions, and a higher exposure to predators (Shumway & Parsons 2006), all of which potentially inflict negative impacts on scallop growth and condition.

Essentially scallops and screwshells can be seen as competing for space resources. Competition for space has been identified as a mechanism affecting distributions of bivalve species in other studies (Frechette & Lafaivre 1990, Josefson 1998). For example, in assessing competition between a bivalve and brittle-star, Josefson (1998) suggested that space may be limiting in soft-sediment systems in which

filter-feeding is a dominating feeding mode, and the input of fresh phytoplankton to the benthos is relatively high. If *P. fumatus* demonstrates preference for bare substratum where it can recess into the sediment while *M. roseus* aggregations are able to take over and smother these areas, then *M. roseus* is able to effectively displace the scallop.

4.5.3 CONCLUSIONS

Both surveys and experiments I conducted indicate a clear preference of *P. fumatus* to occupy bare sediment but not areas of dense 'mats' of screwshells. The result suggests that areas occupied by screwshells at densities greater than 200 m^{-2} are essentially unavailable to support even low densities of *P. fumatus*. Given that *M. roseus* now occupies vast areas of soft sediment benthos along the east coast of Australia, with extensive aggregations existing at densities in excess of 200 m^{-2}, I conclude that extensive areas of previously accessible habitat are now no longer available for occupancy by *P. fumatus*.

Of considerable interest is the potential longevity of impacts from *M. roseus* because both live and dead and empty *M. roseus* shells affect the distribution of all three species of scallop. This highlights that the effects of *M. roseus* on scallops persist after the death of the screwshells. Given the extreme longevity of screwshells in the environment (i.e. they are thick-walled, dense and hard shells, have no known predators as adults, and resistant to boring) their impact is likely to be long-lasting. They do not fragment easily in the environment, even in high energy surf zones. Further, the shell's longevity may be even further enhanced when occupied by

hermit crabs, as the crabs retain the shell above the sediment surface where it is less likely to bioerode (Hazlett 1981, Reiss et al. 2003). Therefore, because impacts of *M. roseus* are not restricted to living shells, and dead and empty shells also impact scallop distribution and behaviors, the impact of *M. roseus* far outlasts the life-span of living shells. Such a marked and sustained impact from this species is likely to have fundamental impacts on the distribution of all three scallop species we assessed, but particularly *P. fumatus*. Given this impact, there is a clear motivation for the development of management options for *M. roseus*, as the exact impact on both commercial and recreation scallop fisheries in SE Australia remains unclear and warrants further investigation.

CHAPTER 5

IMPACTS OF NEW ZEALAND SCREWSHELLS (*MAORICOLPUS ROSEUS*) ON GROWTH AND CONDITION OF JUVENILE COMMERCIAL SCALLOPS (*PECTEN FUMATUS*).

5.1. ABSTRACT

The invasion of SE Australia by the exotic New Zealand screwshell, *Maoricolpus roseus*, has sparked concern over its potential impact on native soft-sediment assemblages and, in particular, on commercially harvested molluscs. Here I quantify the impact of both live and dead and empty *M. roseus* shells on the growth, condition and survival of juvenile commercial scallops, *Pecten fumatus*. In a manipulative experiment, *P. fumatus* juveniles exhibited up to 27% slower linear shell growth, 5% lighter shells (dry weight), 12% less soft-tissue (ash-free dry weight) and 17% poorer condition when caged with live *M. roseus*. Dead and empty screwshells also reduced scallop growth and condition relative to controls, but the extent of the impact depended on scallop density. Scallop mortality did not differ between treatments. The experiment yielded evidence of resource restricted development of *P. fumatus*, which I interpret as competition for both food resources and space with *M. roseus*. Given the wide-spread distribution of *M. roseus* and its potential occurrence at high densities across large areas of seafloor in southeast Australia (Bax et al. 2003, Reid 2003, Gunasekera et al. 2005), impacts on scallop growth and condition have the potential to greatly affect both commercial and recreational scallop fisheries in SE Australia.

5.2. INTRODUCTION

The accelerated introduction of non-indigenous species (NIS) is regarded as a major threat to the integrity and function of natural marine ecosystems worldwide (Carlton et al. 1990, Carlton & Geller 1993, Ruiz et al. 2000, Crooks 2002, Ruiz & Hines 2004). While some NIS expand to significantly impact commercial and recreational fisheries and aquaculture, often with substantial economic repercussions (Hall & Mills 2000), the great majority of NIS do not invoke major changes to native assemblages (Johnson 2007). Given this, and because resources for management of NIS are typically limited (Ross et al. 2002, 2003a), it becomes imperative to prioritize management responses to NIS based, at least in part, on their immediate and potential threat to native assemblages (Byers 2002b, Ross et al. 2002, 2003a). Molluscs in particular have been highly successful invaders of marine environments, as illustrated by species such as the Asian clam *Corbula amurensis* (Carlton et al. 1990, Nichols et al. 1990) and European clam *Corbula gibba* (Currie & Parry 1999, Talman & Keough 2001), among several others.

The New Zealand screwshell, *Maoricolpus roseus* (Quoy and Gaimard, 1834), was first identified in Australian waters by Greenhill in 1963, although anecdotal evidence suggests that *M. roseus* may have arrived as early as the 1920s, accompanying shipments of live oysters from New Zealand (Bax et al. 2003). *Maoricolpus roseus* is now widespread along Australia's south east coast between Tasmania and northern New South Wales, and is highly abundant in Victoria, Bass Strait and south-eastern Tasmania (Allmon et al. 1994, Bax et al. 2003, Reid 2003). The species has invaded numerous habitats over a depth range of 0 - 130 m, where it

occurs at densities of 200 - 2000 m^{-2} (Allmon et al. 1994, Reid 2003). Despite that this NIS has occupied Tasmanian waters for *ca.* 90 years, research into its basic ecology and impacts on native soft-sediment assemblages is lacking.

Maoricolpus roseus may affect native soft-sediment species in several ways including modifying habitat, providing a substratum for settlement of other species, predating upon planktonic larvae, and competing for food and space. Competition with native species is of particular interest, as several commercially important species occupy similar habitats and, like *M. roseus*, are benthic filter feeders. One such species is the commercial scallop, *Pecten fumatus* (Reeve 1852). *Pecten fumatus* and *M. roseus* are both common in eastern Tasmania, and in another study spanning the whole length of the D'Entrecasteaux Channel, were found to co-occur at all 20 sites, both occupying a range of substratum types from mud to coarse sand (Chapter 4). Notably, *M. roseus* shells can occupy the sea floor at densities ~ 1200 m^{-2} when they form an unbroken mat over the sediment, and at densities of ~ 2000 m^{-2} they are amassed as a layer ~ 100 mm deep. Since *P. fumatus* typically recesses into the sediment remaining partially buried for much of the time, reduced access to soft-sedimentary habitat, as a result of proliferation of the screwshell in this way, may also impact growth and condition of *P. fumatus* individuals.

Despite extensive research on NIS in freshwater and terrestrial systems, quantitative experimental data on potential impacts of non-indigenous marine species is typically less comprehensive (Ruiz et al. 1999, Talman & Keough 2001). Moreover, studies addressing impacts of NIS in marine habitats have typically focused more on qualitative observational data obtained through surveys than on quantitative

examination of the mechanisms of impact through the use of controlled experiments (Race 1982, Brenchley & Carlton 1983, Nichols et al. 1990, Grosholz & Ruiz 1995, Talman & Keough 2001, Ross et al. 2002, 2003b). In this paper, I use a manipulative experiment to quantify the impact of *M. roseus* on the growth, condition and survivorship of *P. fumatus* juveniles. I compare impacts associated with live and dead *M. roseus* shells and quantify differences in interspecific and intraspecific competition. This study provides one of the first quantitative assessments of the impact of *M. roseus* on a native species in Australia.

5.3. METHODS

5.3.1 EXPERIMENTAL SITE, SCALLOP TAGGING AND SCREWSHELL COLLECTION

The D'Entrecasteaux Channel is a narrow inlet of the Tasman Sea, extending for ~ 55 km between Bruny Island and the southeast coast of mainland Tasmania. The experiment was conducted *in situ* at Bligh Point on Bruny Island (Fig 5.1), which consists of a shallow rocky reef that descends quickly into a gently sloping soft-sediment bottom dominated by fine sands and shell grit. The experiment was carried out at 12 m depth, where both commercial scallops and screwshells co-occurred at low densities.

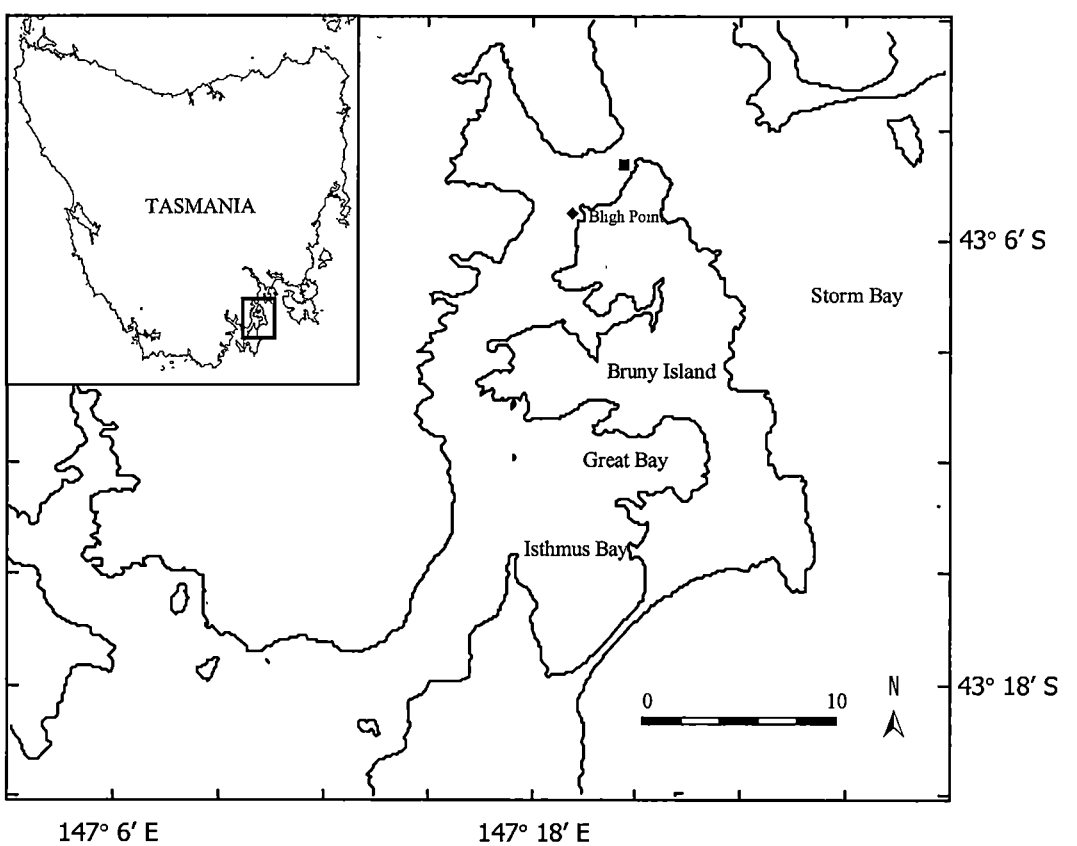

Figure 5.1. Map of the D'Entrecasteaux Channel, Tasmania, showing the location of the study site at Bligh Point (◆) and the screwshell collection site at Dennes Point (■).

Juvenile *Pecten fumatus* were obtained from Jolly Roger Holdings Pty. Ltd., Tasmania, on 18 May 2005, and held in laboratory aquaria with unfiltered flow-through seawater until 21 May 2005. Scallops were individually tagged with a small cylindrical plastic fish tag, cemented into the central groove of the upper valve, using Loctite® 454 Cyanoacrylate. Initial measurements of shell length and width were taken at the same time as tagging, measured to the nearest 0.1 mm using vernier callipers. A digital photograph was also taken of the flat right valve of each scallop prior to deployment.

Maoricolpus roseus were collected at Dennes Point (Fig 5.1) in 12 m of water using a dredge (opening = 630 mm by 350 mm, depth = 320 mm) on 12 May 2005 and held in laboratory aquaria until 14 May 2005. Live *M. roseus* were separated from dead and empty shells, and shells containing hermit crabs. Additional dead and empty *M. roseus* were obtained from Blackman's Bay beach (43' 00.085 S, 147' 19.577 E).

Juvenile scallops approximately 40 mm in width were used in the experiments. They were reproductively immature, which allows any observed impacts on scallop growth and condition (to both soft tissue and the shell) to be interpreted independently of processes associated with directing energy to gametogenesis, or to biomass loss from spawning.

5.3.2 EXPERIMENTAL DESIGN

The experiment was carried out in circular cages consisting of a rigid 60 mm high polyvinylcarbonate (PVC) ring (1 m^2) attached to a ring of oyster mesh (600 mm high and mesh size of 20 x 20 mm). Cages had no roofs or floors, and a small curtain of soft mesh supported by buoys attached to the top of the cages prevented sea stars from entering. Cage walls were sufficiently high to prevent scallops from swimming over the top. Cages were pushed into the sediment to a depth of 80 mm and pinned into place to prevent the escape of scallops and the incursion of predators under the cages. Cages were cleared of any fouling every two weeks.

Screwshells were added to the experimental cages one week before the introduction of scallops to minimise impact to the natural sediment structure. Screwshells were allocated randomly to two treatments: cages with live screwshells added at 1000 m^{-2} and cages with dead and empty screwshells added at 1000 m^{-2}. A control cage, which did not contain any screwshells, was also deployed. Each treatment was applied to 6 individual cages, and each of the six cages in each treatment was then randomly allocated either 5, 10, 15, 20, 25, or 30 *P. fumatus* juveniles. This design allowed both intra- and inter- specific competition to be quantified and allowed definitive separation of impacts of live screwshells (competition for food and space) from impacts related to the physical presence of screwshells alone (competition for space).

The densities of screwshells used in the experiment were similar to those from random quadrat samples undertaken during a pilot survey, and represented natural

densities of screwshells commonly observed in SE Tasmania. Natural densities of adult commercial scallops (shell width >80mm) in the D'Entrecasteaux Channel rarely exceed 4 m^2, although no data are available for juveniles or spat. We note however, that it is not uncommon for scallop spat and juveniles to exceed 100 m^{-2} (or 100 % cover) under aquaculture conditions, with minimal mortality.

The experiment commenced on 21 May 2005 and ran for 85 days. On completion, all surviving scallops were measured for the following parameters: shell width (mm), shell height (mm), right valve growth (mm), dry weight of shell and soft tissue (g) and ash-free dry weight of soft-tissue (g). Right valve growth was calculated as the distance between a clearly visible stress ring, laid down at the time of relocation of the scallops, and the edge of the shell. I assessed whether this metric gave a more precise measure of growth than the change (final - initial) in shell width. Dry weights were calculated by carefully removing soft-tissue from the shell and drying each component separately to a constant weight which was achieved at 60 °C for 48 hrs. Ash-free dry weight of soft-tissue was determined after burning off organic matter for 7 hrs at 500 °C in a blast furnace. A measure of condition was calculated by dividing the ash-free dry weight of soft tissue by the dry weight of the shell for each individual scallop (Lucas & Beninger 1985).

Mortality was assessed weekly, with dead shells removed from their respective cages. Shells that were chipped or broken indicated predation from crabs or octopus as a source of mortality and were recorded accordingly. Because entry of the cages by sea stars was prevented successfully by the design of the cage, dead scallops with

intact undamaged shells, often with residual soft-tissue remaining attached to the shell, were assumed as lost to other sources of mortality.

5.3.3 STATISTICAL ANALYSES

Comparisons of measured parameters among treatments were analysed using a single-factor ANCOVA with screwshell type and density as the fixed treatment factor and scallop density as the covariate. Because measurements of individual scallops within the same cage were not independent, the analysis was conducted on the means for each cage. Regressions fitted to each treatment were initially tested for homogeneity of slopes before proceeding with comparison of the intercepts. All data were examined using box-plots and normal probability plots to ensure the assumptions of normality and homogeneity of variances were satisfied. No transformation was necessary for any parameters. The parameters of shell dry weight, soft-tissue dry weight and soft-tissue ash-free dry weight were standardised by shell width to avoid confounding with variation in scallop size. Weights were only standardised after ensuring that both the relationship between shell weight and shell width, and the relationship between soft-tissue weight and shell width were linear.

5.4. RESULTS

5.4.1. INTRASPECIFIC COMPETITION IN SCALLOPS

There were obvious intraspecific effects on the growth of *P. fumatus*, evidenced by a decline in all of the scallop growth and condition parameters assessed with increasing scallop density in both the control and live screwshell treatments (Fig 5.2). Notably, this was not the case in treatment with dead screwshells, in which the various parameters remained uniformly low with increasing scallop density, at a level similar to that in the highest scallop density in the control (Fig 5.2).

All parameters, except shell dry weight and soft-tissue ash-free dry weight, yielded significant covariate*treatment interactions in the ANCOVA, indicating that slopes were non-homogenous across treatments (Table 5.1). This reflects that growth of scallops was unaffected by scallop density in the treatment with dead screwshells, while in both the control and in the treatment with live screwshells, growth declined significantly, and at a similar rate, with scallop density (Table 5.3). For this reason, individual regressions were fitted to all measured parameters for the dead screwshell treatment (Table 5.2), and the ANCOVAs were repeated using data from the control and live screwshell treatments only (Table 5.3). This enabled means to be compared between the treatments where slopes were found to be homogenous (i.e. in the control and live screwshell treatments).

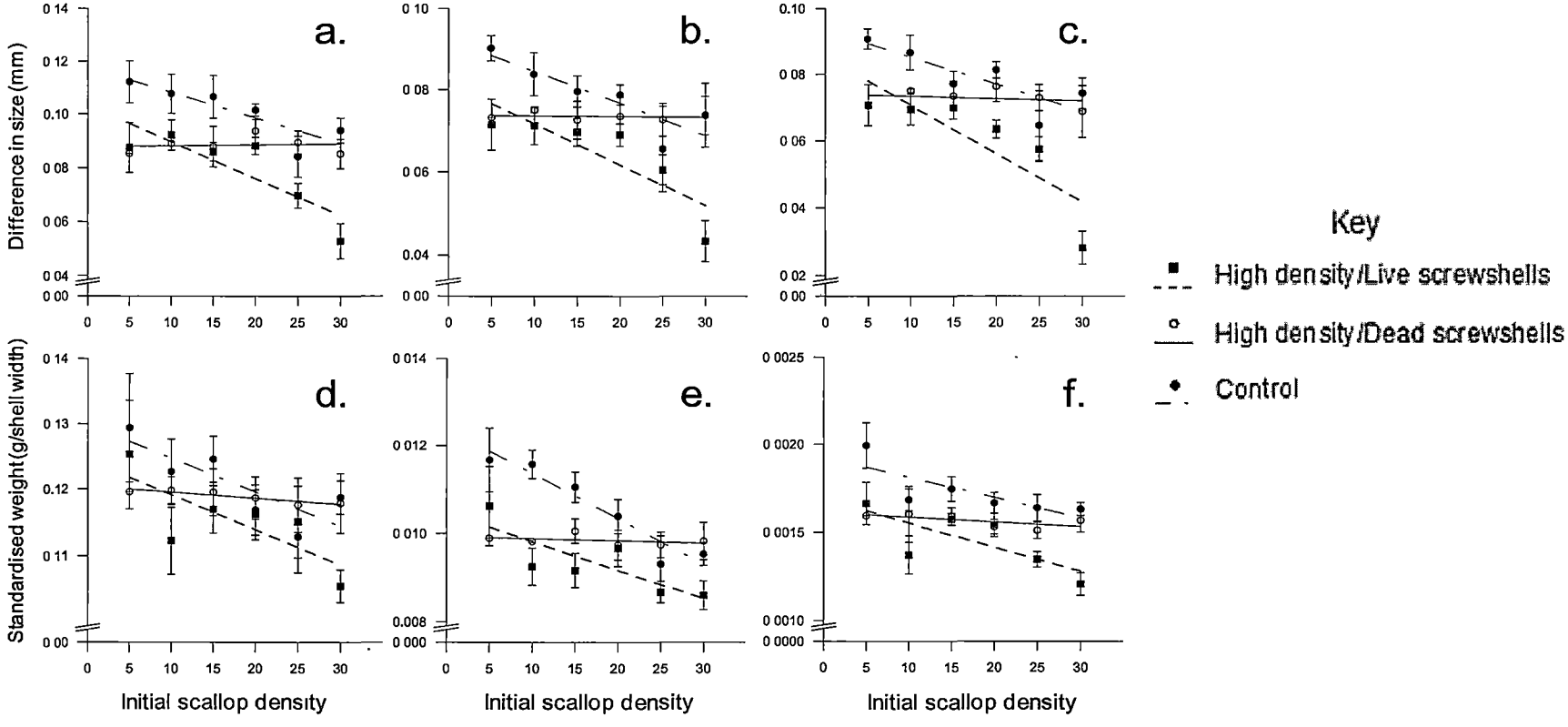

Figure 5.2. Differences in *Pecten fumatus* juveniles under the different treatment conditions and across all initial scallop densities at the conclusion of the experiment. Shell width (a) and shell length (b) were calculated as the difference in scallop size between the start and end of the experiment and right valve growth (c) was calculated by measuring the distance of the right valve from the shell edge to the stress line laid down during deployment. Dry shell weight (d), dry somatic tissue weight (e) and ash-free dry somatic tissue weight (f) were standardised by shell width. All measurements displayed as means ± S.E. for individual cages.

5.4.2 INTERSPECIFIC COMPETITION BETWEEN SCREWSHELLS AND SCALLOPS

The presence of live *M. roseus* had a significant negative effect on scallop growth measured as the change in width and length of the shell, and right valve growth, and on absolute yield expressed as dry shell weight, soft-tissue dry weight, and soft-tissue ash-free dry weight (Fig 5.2). On average, scallops housed with live screwshells exhibited 21% less growth in shell width, 19% less growth in shell height, 27% lower right valve growth, a 5 % loss in shell mass, 12 % loss of soft-tissue mass and carried 18% less ash-free soft-tissue than scallops grown in otherwise identical conditions without screwshells (Fig 5.2, Table 5.3).

Significant differences in the condition of *P. fumatus* juveniles were also detected between the live screwshell treatment and the controls. Independent of the decline in condition of scallops with increasing initial scallop densities, scallops in cages without screwshells were consistently in better condition than those caged with live screwshells. On average, the condition of scallops cohabiting with live screwshells was 12% lower than that in the controls (Fig 5.3).

Table 5.1. Analysis of covariance (ANCOVA) results of all measured scallop parameters of *P. fumatus* in all treatments. Bold values indicate P<0.05.

Source of variation	df	Mean square	*F*	p
Shell width (mm/day)				
treatment	2	0.00025791	5.96	**0.0159**
scallops	1	0.00076141	17.61	**0.0012**
treatment*scallops	2	0.00022707	5.25	**0.023**
Shell length (mm/day)				
treatment	2	0.00010165	4.64	**0.0321**
scallops	1	0.00046732	21.34	**0.0006**
treatment*scallops	2	0.00011636	5.31	**0.0222**
Right valve growth (mm/day)				
treatment	2	0.0001128	2.34	0.1386
scallops	1	0.00079281	16.45	**0.0016**
treatment*scallops	2	0.00020976	4.35	**0.0379**
Shell dry weight (g)				
treatment	2	0.00002582	2.09	0.1662
scallops	1	0.00018778	15.21	**0.0021**
treatment*scallops	2	0.00002672	2.16	0.1575
Soft-tissue dry weight (g)				
treatment	2	1.92×10^{-6}	16.12	**0.0004**
scallops	1	4.30×10^{-6}	36.07	**<0.0001**
treatment*scallops	2	1.07×10^{-6}	8.97	**0.0041**
Soft-tissue ash-free dry weight (g)				
treatment	2	3.20×10^{-8}	3.75	0.0544
scallops	1	1.12×10^{-7}	12.95	**0.0037**
treatment*scallops	2	1.50×10^{-8}	1.75	0.2147

Table 5.2. Regression results of all growth parameters of *P. fumatus* in the treatments with dead screwshells. Note that none of the parameters varied significantly with scallop density. Bold values indicate P<0.05.

Parameter measured	Regression	r^2	*t value*	p
Shell width (mm/day)	$SW = -3.57 \times 10^{-5}(SD) + 0.088$	0.0113	0.21	0.841
Shell length (mm/day)	$SL = -1.30 \times 10^{-5}(SD) + 0.074$	0.0187	-0.28	0.7961
Right valve growth (mm/day)	$RVG = -6.17 \times 10^{-5}(SD) + 0.074$	0.0421	-0.42	0.6965
Shell dry weight (g)	$SDW = -5.86 \times 10^{-5}(SD) + 0.120$	0.5095	-2 04	0.1111
Soft-tissue dry weight (g)	$STDW = -4.49 \times 10^{-6}(SD) + 0.010$	0.1355	-0.79	0.4729
Soft-tissue ash-free dry weight (g)	$STAFDW = -2.51 \times 10^{-6}(SD) + 0.006$	0.4343	-1.75	0 1546

Table 5.3. Analysis of covariance (ANCOVA) results of all parameters of growth and condition of *P. fumatus* in control and live screwshell treatments. 'Scallops' refers to scallop density. Bold values indicate P<0.05.

	Test for homogenous slopes				Test for intercepts			
Source of variation	df	Mean square	*F*	p	df	Mean square	*F*	p
Shell width (mm/day)								
treatment	1	0.00011983	2.04	0.1912	1	0.00140033	24.84	**0.0008**
scallops	1	0.00117804	20.04	**0.0021**	1	0.00117804	20.9	**0.0013**
treatment*scallops	1	0.00003696	0.63	0.4507				
Shell length (mm/day)								
treatment	1	0.00006813	2.11	0.1848	1	0.00062626	21.03	**0.0013**
scallops	1	0.00069082	21.35	**0.0017**	1	0.00069082	23.2	**0.001**
treatment*scallops	1	0.00000916	0.28	0.6091				
Right valve growth (mm/day)								
treatment	1	0.00004175	0.62	0.4544	1	0.00112031	16.16	**0.003**
scallops	1	0.00112707	16.68	**0.0035**	1	0.00112707	16.25	**0.003**
treatment*scallops	1	0.00008358	1.24	0.2983				
Shell dry weight (g)								
treatment	1	0.00001742	0.95	0.3593	1	0.00009559	5.84	**0.0389**
scallops	1	0.00023743	12.89	**0.0071**	1	0.00023743	14.5	**0.0042**
treatment*scallops	1	0.00000002	0	0.9771				
Soft-tissue dry weight (g)								
treatment	1	2.12×10^{-6}	12.37	**0.0079**	1	4.74×10^{-6}	16.12	**0.0007**
scallops	1	6.11×10^{-6}	35.61	**0.0003**	1	6.11×10^{-6}	32.63	**0.0003**
treatment*scallops	1	3.13×10^{-6}	1.82	0.2141				
Soft-tissue ash-free dry weight (g)								
treatment	1	3.38×10^{-8}	2.74	0.1366	1	2.27×10^{-7}	20.53	**0.0014**
scallops	1	1.37×10^{-7}	11.08	**0.0104**	1	1.37×10^{-7}	12.37	**0.0065**
treatment*scallops	1	7.85×10^{-10}	0.06	0.8075				

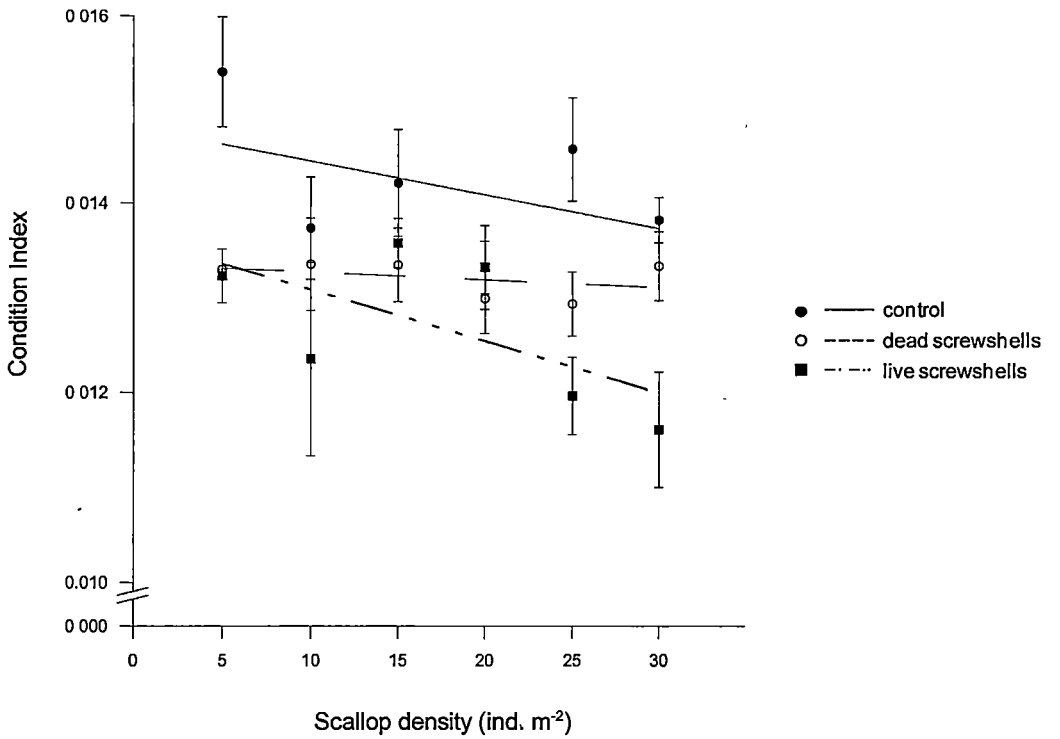

Figure 5.3. Condition of *Pecten fumatus* juveniles under the Control (●), Dead screwshell (o) and Live screwshell (■) treatments and across all scallop densities. Regression analysis on the dead screwshell treatment indicated that the slope was not significantly different from zero (Regression: $F_{1,1}$= 0.09, P = 0.779). ANCOVA carried out between the control and live screwshell treatments alone indicated significant differences in intercepts between the two treatments (ANCOVA, test for homogenous slopes, treatment*scallop interaction: $F_{1,2}$ = 0.14, P = 0.713, test of intercepts, Treatment: $F_{1,1}$ = 14.44, P = 0.004, Scallop density: $F_{1,2}$ = 3.83, P = 0.082)

The presence of dead and empty *M. roseus* shells also resulted in reduced growth of *P. fumatus* juveniles, at least at low scallop densities (Fig 5.2). Scallops cohabiting with dead screwshells showed similar growth, irrespective of initial scallop densities, with all parameters yielding a slope not significantly different from zero (Table 5.2). It follows that at low initial scallop densities (5-10 m^{-2}), growth and yield of scallops in the presence of high densities of dead screwshells was markedly lower than when screwshells were absent. However, at high initial scallop densities

(25-30 m^{-2}), any effect of dead screwshells on the growth and yield of scallops was much less evident (Fig 5.2). A similar pattern was evident when considering the overall condition of scallops (Fig 5.3).

5.4.3 SCALLOP MORTALITY

There was no clear evidence of any effect of either live or dead *M. roseus* on survivorship of *P. fumatus* juveniles. Of 315 juvenile *P. fumatus* deployed initially, a total of 266 (84.5%) were recovered by the completion of the experiment. Of those recovered, 214 were alive after 85 days, and 52 were recovered over the course of the experiment having suffered some form of mortality. There was no clear effect of any treatment on the number of scallops lost to the different types of mortality, although there was a trend of higher mortality associated with predation and 'other' sources of mortality in high scallop densities in treatments with screwshells (Fig 5.4).

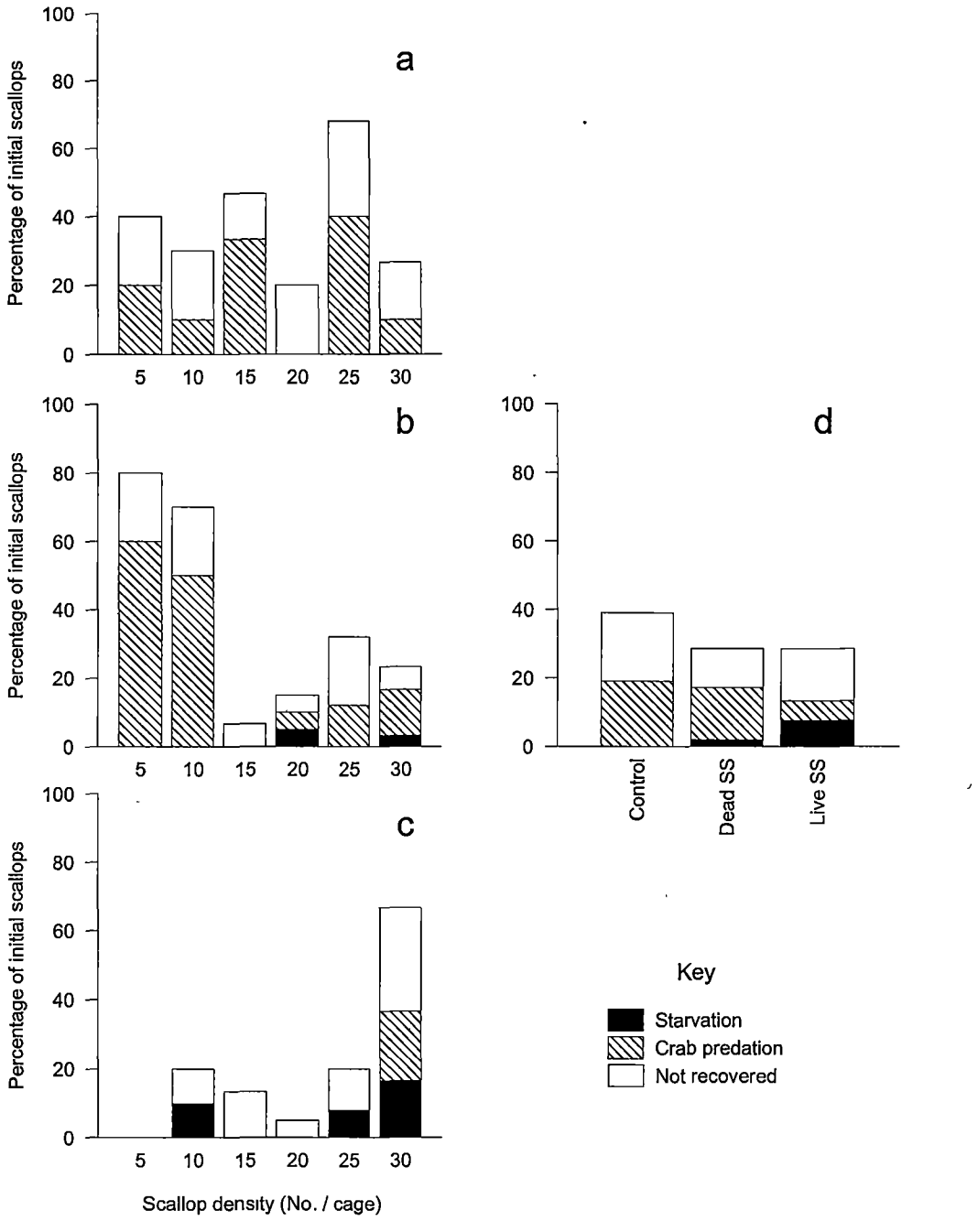

Figure 5.4. Number of scallops lost to different sources of mortality in the Control (a), Dead screwshell (b) and Live screwshell (c) treatments. (d) depicts the losses to the different sources of mortalities for all three treatments, pooled across all initial scallop densities.

5.5. DISCUSSION

The accelerated introduction of non-indigenous marine species is regarded as a major threat to the integrity and function of natural marine ecosystems worldwide (Carlton et al. 1990, Carlton & Geller 1993, Carlton 1996b, a, Cohen & Carlton 1998, Ruiz et al. 1999, Ruiz et al. 2000, Crooks 2002, Ross et al. 2002, 2003b, a, Ruiz & Hines 2004). Due to limited resources available to combat introduced marine species, it is becoming increasingly more accepted that management must involve prioritization of introduced species based on their immediate and potential threat to native assemblages (Byers 2002b, Ross et al. 2002, 2003b). A potentially devastating impact of introduced species is their impact on the growth and development of commercially important species, often with substantial economic repercussions (Hall & Mills 2000). Therefore, the prioritisation of management for introduced species must include as estimate of impact to commercially important species.

5.5.1 INTRASPECIFIC AND INTERSPECIFIC COMPETITION

Intraspecific effects on growth have been well documented in bivalves (Peterson 1979, Peterson & Black 1987, 1988, Peterson & Beal 1989, Frechette & Daigle 2002), and have often been considered more important than interspecific effects in governing growth and development of individual bivalves (Peterson & Beal 1989) and whole populations (Weinberg 1985, 1998). The present work demonstrated a linear reduction in all scallop parameters of growth and condition indicating an intraspecific density-dependent effect on *P. fumatus* growth and condition in the absence of screwshells. In fact, over the full array of scallop densities used in the

experiment (5 – 30 m^{-2}), intraspecific effects appeared to be greater than interspecific impacts in most, if not all, scallop parameters of growth and condition. However, considering that natural densities of juvenile *P. fumatus* are rarely likely to exceed 10 m^{-2}, interpretation of impacts only at low densities of scallops (5-10 m^{-2}) indicates that interspecific effects are likely to be greater than intraspecific effects.

Natural densities of live *M. roseus* had a significant impact on the growth and condition of *P. fumatus* juveniles indicating a definite interspecific impact. The magnitude of the effect was consistent across all initial scallop densities (5-30 m^{-2}) The presence of either live or and dead and empty *M. roseus* shells greatly reduced the growth and condition of juvenile *P. fumatus*. Similar results were reported from experiments in which *P. fumatus* were caged with an exotic bivalve *Corbula gibba* (Talman & Keough 2001).

5.5.2 POTENTIAL MECHANISMS OF IMPACT

5.5.2.1 Reduced food quantity

The reduced growth and condition of scallops observed in the treatment with live screwshells can be partially explained by a restriction in food supply. Restricted seston quantity and quality is often suggested to account for density-dependent effects observed in many bivalves (Peterson & Black 1987, 1988, Peterson & Beal 1989, Rheault & Rice 1996), including scallops (Pilditch & Grant 1999a, b). This could partially explain both the intra and interspecific effects observed in our experiment. Depletion of benthic and pelagic phytoplankton within the benthic boundary layer and the subsequent competition between individuals for food

resources has been demonstrated in many suspension feeding species (Wildish & Kristmanson 1984, Frechette & Bourget 1985, Wildish et al. 1992, Jensen 1993, Josefson 1998, Wildish 2001), and at scales as large as whole estuaries (e.g. Nichols et al. 1990, Strayer et al. 1999a).

If a reduction in seston quantity is to account for the reduced growth of scallops, this would require utilization of similar food resources by both *P. fumatus* and *M. roseus*. *Maoricolpus roseus* is capable of filtering particles 8-75 μm in size (Tobias Probst, Pers. Comm.), although quantitative estimates of clearance rates and assimilation efficiencies of this species have only been determined for particles <10 μm (Scott 1997). Scallops, in general, are capable of retaining particles 2-350 μm in size, although 100% retention efficiency is attained only with particles exceeding 5-7 μm in size, and efficiency declines for particle sizes less than this (Shumway and Parsons, 2006 and references therein). Clearance rates of screwshells range from 0.102 – 0.290 $l.h^{-1}.gDW^{-1}$ (Scott 1997) dependent on particle concentration, and although quantitative estimates of clearance rates and assimilation efficiency for *P. fumatus* are unavailable, a similar scallop species, *Placopecten magellanicus*, exhibits clearance rates of 0.871 - 1.318 $l.h^{-1}.g.DW^{-1}$ (MacDonald & Thompson 1986). Given the strong overlap in particle size used by both species, the reduced growth in scallops cohabiting with live screwshells could be attributed, at least in part, to competition for food.

Benthic sources of phytoplankton can also be important to growth and development in scallop species (Shumway et al. 1987, Grant et al. 1997). While benthic resources

in the form of detritus and benthic microalgae cannot alone sustain scallop growth and development (Cranford & Grant 1990, Grant & Cranford 1991), they are nonetheless an important source of nutrition for scallops, particularly when phytoplankton availability is low (Grant et al. 1997, Shumway & Parsons 2006). In this context it is important to note that *M. roseus* may be capable of both suspension feeding and deposit feeding (Bax et al. 2003). The purported ability to switch feeding modes suggests that *M. roseus* might reduce growth in *P. fumatus* by depleting both pelagic and benthic food sources. However, I note that the relative importance of the two feeding mechanisms employed by *M. roseus* is yet to be determined. Moreover, better quantitative estimates of site-specific consumption of pelagic and benthic particles by both *M. roseus* and *P. fumatus* are necessary to establish evidence of reduced benthic resources as a mechanism of impact.

5.5.2.2 Reduced food quality

High densities of *M. roseus* may also affect *P. fumatus* growth by reducing the quality of food resources, or interfering with the scallop feeding and respiratory apparatus (Grant & Thorpe 1991) Both could arise as a secondary impact of the expulsion of large quantities of pseudo-faeces by the screwshell. This effect has been suggested impact other bivalve species (Talman & Keough 2001). If pseudo-faecal exudates are not easily re-suspended, the contents are simply removed from the available pool (Grant et al. 1997), directly reducing the quantity of resources available for consumption. Even if they are readily re-suspended, plankton exudates in re-suspended pseudo-faeces are likely to have highly altered nutritional value and chemical composition.

5.5.2.3 Competition for space

Competition for space is also likely to contribute to reduced growth rates of *P. fumatus* as evident by clear reductions in scallop growth and condition of *P. fumatus* juveniles caged with high densities of dead and empty screwshells. The effect of screwshells was more evident at low densities of scallops (5-10 ind. m^{-2}). Conversely, at high initial scallop densities (25-30 ind. m^{-2}), there was no evidence of restricted growth and development of scallops in the presence of dead screwshells. This suggests that at low scallop densities competition with screwshells for space reduces scallop growth and condition, while at high scallop densities intraspecific competition between juvenile scallops associated with food acquisition outweighs any effect of interspecific competition for space.

The reduced growth and condition observed in the dead and empty screwshell treatment suggests the possibility of a higher energy expenditure of these scallops. *Pecten fumatus* is a species that 'recesses' or partially buries into the sediment, possibly in order to optimise feeding currents (Kirby-Smith 1972, Wildish et al. 1987, Wildish & Kristmanson 1988, Wildish & Saulnier 1992, 1993, Pilditch & Grant 1999b), minimize predation (Shumway & Parsons 2006), and/or assist in expulsion of pseudo-faeces. In areas where screwshells 'mat' the surface, it is probable that scallops will continue to swim in order to attain a clear area of benthos in which to recess (Chapter 4). This will increase energy use, and other studies have noted that it may take bivalves several hours to recover from swimming (Thompson et al. 1980, Brokordt et al. 2000a, Brokordt et al. 2000b). This, compounded by less time spent filter-feeding because of increased swimming, may ultimately reduce

scallop growth rates and condition. Further, scallops unable to recess, or positioned on top of screwshell 'mats' may have to deal with sub-optimal current speeds and turbulence (Kirby-Smith 1972, Wildish et al. 1987, Wildish & Kristmanson 1988, Wildish & Saulnier 1992, 1993, Pilditch & Grant 1999b), atypical boundary layer conditions (Wildish 2001) and a higher exposure to predators (Shumway & Parsons 2006), all of which could inflict negative impacts on growth and condition.

5.5.2.4 Evidence of multiple mechanisms of impact

Identifying the mechanisms by which *M. roseus* impacts scallop growth and condition is aided by comparing responses to the treatment containing live screwshells with that of dead and empty screwshells. More specifically, effects in the treatment with live screwshells are likely to reflect a combination of interspecific competition for food and space, whereas the treatment with dead and empty shells is likely to reflect effects solely associated with interspecific competition for space. Moreover, any observed effects in control cages can only result from intraspecific interactions.

Given the significant effects identified in all experimental treatments (including the control), there is clear evidence that intraspecific competition for food between *P. fumatus* individuals, interspecific competition for food between *P. fumatus* and *M. roseus* and interspecific competition for space all contribute, at least in part, to explaining the observed treatment effects.

5.5.3 SCALLOP MORTALITY

The experiment failed to detect differences between the treatments with respect to the rate and types of mortality experienced by juvenile *P. fumatus*. However, given that cages were designed to restrict access of potential scallop predators, it is not surprising only ~15 % of *P. fumatus* juveniles were recovered having suffered some form of mortality. The result may be an artifact of predator exclusion; if there is differential predation in the presence and absence of screwshells, then the current design will not detect this. Regarding sources of mortality not related to predation, some studies have described starvation of bivalves in high densities, although death via resource limitation appears to be very uncommon (Peterson 1982, Talman & Keough 2001).

5.4 CAVEATS AND CONCLUSIONS

Maintenance of treatment densities of both *M. roseus* and *P. fumatus* required the use of artificial cages. A potential problem in using cages is that they potentially create artifacts that do not arise under natural conditions. In particular, altered current flows and development of a fouling community on the mesh walls of cages have been shown to slow growth of some bivalves by reducing the supply of seston (Claereboudt et al. 1994, Harrison et al. 1996). However, the large mesh size used in this experiment would have minimized alteration to current flows and turbulence, and fortnightly cleaning of the cages prohibited development of macroscopic fouling community on the cage walls.

Use of circular cages in this experiment alleviated effects of cage corners, and scallops appeared to utilize the full area provided with no obvious association with cage walls. Further, the lack of a cage floor and roof enabled scallops and screwshells to 'recess' into the sediment, and allowed motile fauna (other than seastars, which were excluded by a curtain of soft-mesh) to enter through the top of the cages without interference.

Many concerns have been raised regarding the establishment of *M. roseus* in SE Australia, and its potential impact on native soft-sediment assemblages. This experiment yields strong evidence that the growth, development and condition of the commercially important scallop species, *Pecten fumatus*, is significantly reduced by the presence of both dead and live *M. roseus* shells. The most prominent of impact is likely interspecific competition for food, however, there is also clear evidence that the physical presence of *M. roseus* independent of their feeding also resulted in reduced growth and condition of scallops. The latter may result from higher metabolic costs associated with scallops swimming in an attempt to find clear sediment 'patches' in which they are able to recess. *Pecten fumatus* shows obvious preferences for bare sediment over benthos dominated by screwshells, as evident from results of Chapter 4. It seems certain that the impact of *M. roseus* on scallop growth and condition extends further than only areas occupied by live *M. roseus*, and includes accumulations of dead screwshells. Further, dead screwshell accumulations may persist for lengthy periods of time and as a result, impacts associated directly with the physical presence of *M. roseus* shells may continue well past the life-span of live screwshells. Furthermore, given the potentially vast

distribution of high densities of *M. roseus* in SE Australia, a large areas of seafloor is now potentially sub-optimal habitat for *P. fumatus*. This indicates that the effect of the screwshell on potential scallop fisheries in SE Australia has already been significant.

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CHAPTER 6

GENERAL DISCUSSION

6.1 NON-INDIGENOUS SPECIES

The human-mediated introduction and natural range expansion of NIS is considered a significant force of ecological change in both terrestrial and aquatic systems and is regarded as major threat to the integrity, diversity and health of natural ecosystems worldwide (Carlton et al. 1990, Carlton & Geller 1993, Carlton 1996b, a, Cohen & Carlton 1998, Ruiz et al. 1999, Ruiz et al. 2000, Crooks 2002, Ross et al. 2002, 2003b, a, Ruiz & Hines 2004). The actual and potential impact arising from the establishment of NIS is however, highly variable. In some instances, the impact to recipient communities from the invasion of an exotic species has been extreme, as illustrated by the invasion of San Francisco Bay by the Asian clam *Corbula amurensis* (Carlton et al. 1990), (Nichols et al. 1990) the spread of the ctenophore *Mnemiopsis leidyi* throughout the Black and Caspian seas (Shiganova 1998, Kideys 2002), among several others. In other instances, the exotic species invokes only minor changes to the natural ecosystem, or even exist cryptically (see reviews by Johnson 2007, Schaffelke & Hewitt 2007).

Given only a few of all introduced species necessarily alter the structure or function of their recipient communities or invoke significant ecological change, and that resources for effective responses to NIS are invariably limited, it is imperative that

NIS are prioritized for management based upon the most current and scientifically robust estimate of their imminent and potential impact to native assemblages and habitats (Byers 2002b, Ross et al. 2002, 2003b, a).

A major challenge is how to rigorously assess the immediate and potential impacts of a NIS that also includes information across a number of spatial and temporal scales and at multiple levels of biological organisation (Parker et al. 1999, Ruiz et al. 1999, Crooks 2002, Ross et al. 2003a). Typically, most assessments of impact(s) of NIS have involved only one approach conducted at a single level of biological organisation. This may be due to logistical constraints of time and funding, or simply because the specific research question(s) can be answered by addressing single space-time scales at a single level of biological organisation. Nonetheless, combining information from independent assessments conducted across several scales and levels will enable a more holistic picture of impact.

There have been several good examples of approaches using multiple methods at multiple scales that have been implemented successfully in assessing impacts of NIS (Parker et al. 1999, Ruiz et al. 1999, Crooks 2002, Ross et al. 2003a). Ross et al. (2003a) is a pertinent example, in which impacts of the Northern Pacific seastar (*Asterias amurensis*) were quantified at a variety of spatial and temporal scales in a comprehensive assessment of the seastar's overall impact. This paper highlights the importance of assessing impacts at multiple scales which, when considered simultaneously, can provide added information and interpretation not attainable if the effects at single scales are considered in isolation. The approach not only allows

for variability of impacts across space and time to be appreciated, but it invariably enables accumulation of information from several independent lines of evidence, which brings greater strength and confidence to interpretation of impacts.

In this thesis, I adopted an integrated approach involving multiple methodologies to overcome the shortfalls of using any one approach. While it was possible to collate information across spatial and temporal scales to a certain degree, the main strength of the work has been in tackling impacts of *M. roseus* at different biological levels of organization, i.e. across the levels of the community (Chapter 2), ecosystem process (Chapter 3) population (Chapter 4) and individual (Chapters 4 and 5). A further feature of the work is assessment of the independent effects of different screwshell 'states', i.e. alive shells vs. dead and empty shells vs. dead shells supporting hermit crabs. Given that depending on the area, screwshell accumulations may consist primarily of live individuals (95 % alive), or mostly dead screwshells, the benthic habitat is likely to represent a mosaic of patchily distributed accumulations of screwshells comprising the different screwshell 'states'. As a result, separating the impacts of screwshells in different 'states' elucidated how the impact may vary across this spatial and temporal patchiness of screwshell accumulations observed in nature (see section 6.4).

6.2 Quantifying Impacts at Multiple Levels of Biological Organisation

The level of biological organisation at which ecologists elect to conduct research is often determined by economic imperatives, or pre-existing interest in or perception of impact at a particular level. Thus, research questions may relate to impacts on

native species of particular interest, in which single species or population dynamic approaches may be most appropriate. Alternatively, assessments at a community level or ecosystem level may be necessary when the research question is to address how native systems may be altered in future invasions (Parker et al. 1999, Crooks 2002).

In this work, results from the community-level experiments identified that the physical habitat and infaunal community structure were vastly different in areas supporting *M. roseus* compared with patches of benthos without screwshells. The presence of screwshells (particularly at high densities) resulted in a highly modified community composition, primarily due to significant increase in species richness, species diversity and total macro-invertebrate abundance (Chapter 2). The most significant impact was a marked increase in the epifaunal community growing on the hard substratum provided by *M. roseus* shells, including stone corals, bryozoans, chitons and oysters (Chapter 2).

An increase in abundance of macro-invertebrates and species richness following the invasion of a new environment by an invasive species is not an uncommon phenomenon (e.g. Castel et al. 1989, Posey et al. 1993, Crooks 1998b, Crooks & Khim 1999, Haynes et al. 1999, Horvath et al. 1999, Hedge & Kriwoken 2000). A plethora of mechanisms have been forwarded to explain the dramatic alteration to community structure following the arrival of a NIS, including increased development of 3-dimensional structure (Castel et al. 1989, Stewart & Haynes 1994, Crooks 1998b, Horvath et al. 1999), alteration to sediment size structure or stability

or disturbance (Vitousek 1990, Lenihan 1999, Crooks 2002), changes to water characteristics and organic matter deposition (Crooks & Khim 1999), and interference with biogeochemical cycling, oxygen concentrations and nutrient fluxes (Vitousek 1990, Crooks & Khim 1999, Parker et al. 1999). There is also good evidence that species interactions involving NIS such as competition, predation and facilitation can be important in altering infaunal community structure (see reviews by Byers 2009, Grosholz & Ruiz 2009, Rilov 2009).

Conducting assessments at a community level can be logistically expensive, take extensive periods of time and require large experiments if effects of the NIS are to be isolated from potentially confounding factors. However, there are specific advantages of assessing impacts at the community level. In particular, identifying alterations to the structure of native assemblages due to a NIS can be extrapolated to estimate how new areas may be affected as the distribution of the NIS expands. Evidence from Chapter 2 suggests that should *M. roseus* invade new soft-sediment habitats in SE Australia, the invaded community is likely to realise increased species richness, species diversity and total macro-invertebrates abundance, and develop a diverse epifaunal community. Moreover, the impact is likely to be indefinite as *M. roseus* accumulations progress from being dominated by living shells to domination by dead shells, whether inhabited by hermit crabs or not (discussed in section 6.4).

Focus on population- and individual-level assessments can be particularly useful when it is necessary to assess the impacts of a NIS on particular species, such as those of commercial importance. Population- and individual-level approaches

employed to assess impacts of *M. roseus* on commercial scallop species (primarily *Pecten fumatus*) indicated that the distribution of *P. fumatus* was strongly related to the distribution of *M. roseus*. In general, areas that supported moderate to high densities of screwshells (>200 m^{-2}) failed to support populations of *P. fumatus*, and the species was most abundant in areas devoid of the screwshells, and where the sediment profile was dominated by coarse grains.

In these approaches, the results indicated that *M. roseus* had a significant detrimental impact on *P. fumatus* distribution (Chapter 4), as well as on growth, condition and survivorship (Chapter 5). The population and individual level approaches used to address impacts on *P. fumatus* were logistically straight forward, results were attained in much less time than for the comprehensive community level assessments, and the experiments enabled isolation and identification of specific mechanisms by which *M. roseus* impacts *P. fumatus*. The combination of surveys and *in situ* experiments identified that the most likely mechanisms by which *M. roseus* impacted *P. fumatus* were competition (for both food and space resources) and the significant alteration to the physical 3-D habitat. Identifying the mechanism of impact is not only important in providing information for developing management strategies to combat or adapt to NIS, but it may also assist in management of important recreational and commercial fisheries affected by NIS.

6.3 QUANTIFYING STRUCTURAL AND FUNCTIONAL IMPACTS ON WHOLE COMMUNITIES

Community-level assessments of impacts of NIS on marine benthic systems have typically revolved around defining alterations to habitat structure, infaunal

community structure, and/or the abundance of taxa of special interest (e.g. Castel et al. 1989, Stewart & Haynes 1994, Creese et al. 1997, Crooks 1998a, Crooks & Khim 1999, Horvath et al. 1999, Strayer et al. 1999b, Hedge & Kriwoken 2000, Schwindt et al. 2001). However, the effect of a NIS on ecosystem processes is becoming increasingly recognized as a fundamental aspect of its impact (Grosholz & Ruiz 2009).

Impacts on ecosystem functioning are generally inferred from changes in community structure, and particularly from changes in the abundance of dominant functional groups, rather than measured directly. However, inference in this way is much less certain than direct measurements and, indeed, may simply be erroneous given that community function (often represented by nitrogen, oxygen or carbon flux) is the result of a combination of complex biogeochemical reactions involving several biotic and abiotic interactions among functional groups and that community structure and function are not necessarily strongly correlated. Thus, large alterations to community structure may not necessarily manifest as large alterations in community functioning, while relatively minor alterations to the abundances of a small number of specific functional groups may grossly change the functioning of a community depending on the nature of interactions among species among other things. The most robust approach is to measure impacts of NIS on ecosystem functioning directly, and in parallel with impacts on community structure.

In chapters 2 and 3 the impacts of *M. roseus* on both faunal community structure and function (respectively) were quantified. Community structure in areas of

benthos occupied by even low densities of *M. roseus* was markedly different to similar adjacent areas without the screwshell (Chapter 2 and discussed in section 6.2). Similarly, community metabolism (measured as rates of oxygen flux) was also highly differentiated among areas with and without screwshells. Generally, metabolism was elevated in the presence of screwshells, with higher rates of production and respiration in areas occupied by screwshells, although the effect was strongly dependent upon whether shells were alive, dead and empty, or supporting hermit crabs (Chapter 3). However, despite effects on community function from living shells being vastly different to that of dead and empty shells, faunal communities associated with each of these two screwshell states were relatively similar. Hence, community structure was not always directly correlated with community function (Chapter 2, Chapter 3). Clearly then, direct quantitative measurement of NIS on community function provides a more comprehensive picture of overall impact than estimating changes to community structure alone, and inferring effects on functioning.

6.4 THE IMMEDIATE AND POTENTIAL THREAT OF M. ROSEUS TO NATIVE SYSTEMS

The impact of *M. roseus* on native soft-sediment assemblages is likely to be massive. The results provide strong evidence of small and large scale impacts of *M. roseus* on whole communities, and on individual species of commercial interest. The immediate threat of *M. roseus* to native soft-sediment communities is clearly very high. However, the observed impacts depended not only on the density of the shells, but also on their physical state (i.e. whether they were alive, dead or supporting hermit crabs). In recognising that effects of living shells represent relatively short-

term or immediate impacts, and effects of dead shells represent longer-term impacts past the life of living *M. roseus*, separating the effects of alive and dead shells elucidates how impacts may vary spatially and temporally.

This approach has illuminated two unique facets of the impact of *M. roseus* on native soft-sediment communities. Firstly, because dead shells also have significant effects, impacts are likely to be long lasting given that the persistence of *M. roseus* shells is very high. They are thick-walled, resistant to predation and do not easily fragment, even in high energy surf zones. In at least one study of bivalve shell bio-erosion in New Zealand, some intact, but eroded shells were aged at between 350 - 1320 yrs old, and estimates of destruction by bio-erosion were estimated at between 100' to 1000's of years (Smith 2003). While these were bivalve shells, they do nonetheless provide some indication of the potential rates of bio-erosion in *M. roseus* shells. Moreover, a shell's longevity may also be further prolonged when it is inhabited by hermit crabs, as crabs retain the shell above the sediment surface where it is less likely to bio-erode (Hazlett 1981, Reiss et al. 2003). Therefore, impacts of *M. roseus* will at least outlast the life-span of living shells, and the persistent nature of the shells suggests that even without further recruitment, impacts may persist for centuries, or millennia, particularly in the presence of hermit crabs.

Secondly, the impact of *M. roseus* is likely to highly vary spatially and temporally, because the impacts observed are effectively governed by the relative proportions of live to dead screwshells within accumulations. As screwshell accumulations vary

spatially, and to some degree temporally, one can potentially estimate the likely degree and type of impact expected for a given area of benthos, depending on the screwshell 'state' most dominate in the accumulation. For example, newly invaded communities with low densities of living screwshells are likely to exhibit infaunal communities similar to adjacent areas of bare sediment. The community is likely to exhibit filter-feeding molluscs but due to the relatively recent arrival of the species, epifaunal taxa such as bryozoans, chitons, sponges and stone corals may be depauparate. Moreover, the oxygen flux of the benthos will more likely reflect that of adjacent areas of bare sediment, but may utilise slightly elevated levels of oxygen due to the presence of the screwshells.

After several years of successful recruitment, the density of shells in some soft-sediment locations is likely to increase to well in excess of 1000 m^{-2} consisting almost totally of living shells, and the benthic community structure is likely to undergo major concomitant change. The community will become dominated by epifaunal taxa, particularly bryozoans, sponges and stone corals, and crustacean and polychaete taxa are likely to become significantly more abundant. The oxygen requirements of the benthos will increase significantly, as the energy demands of the living screwshells, and the elevated abundances of epifauna and infauna, combine to become significantly higher than adjacent soft-sediment patches without screwshells. Depending on depth, oxygen requirements of the benthos may be slightly offset by higher local oxygen production associated with increased biomasses of both macro- and micro- algae attached to the shells and within the

sediments, although the benthos is likely to retain a relative net negative oxygen flux.

Other areas of benthos are likely to be dominated by dead and empty shells. This may be because they are sites of deposition and have slowly accrued dead shells over a period of time due to prevailing water currents, or because conditions have not been conducive to *M. roseus* recruitment for an extended period. None-the-less, large-scale accumulations constituted almost solely of dead *M. roseus* are observed under natural conditions. While high density aggregations of living shells only exhibit small differences community structure to high density accumulations of dead and empty shells (Chapter 2), the different accumulation 'types' are likely to display to highly significant differences in the functioning of the community (Chapter 3). Structurally, communities in areas dominated by dead shells will exhibit lower abundances of errant and sedentary polychaetes and predatory gastropods, but heightened abundances of amphipods compared to areas with living *M. roseus*. However, the community will likely be far less energy (oxygen) demanding than those with living shells, due to the absence of living *M. roseus*, which are largely responsible for the respiratory demands of the community. Rates of production however, are likely to be similar irrespective of whether accumulations consist primarily of living or dead screwshells. None-the-less, compared to bare sediments, areas occupied by dead shells will still be more oxygen demanding.

A further complication is that accumulations of the dead shells may become occupied by hermit crabs. In habitats where this occurs, the impact will again differ from areas of benthos dominated by living shells and dead and empty shells. Firstly Hermit crabs are likely to prolong a shell's longevity, as the crabs retain the shell above the sediment surface where it is less likely to bio-erode (Hazlett 1981, Reiss et al. 2003). Secondly, while evidence from Chapter 3 indicates these areas of benthos will have similar oxygen flux to those inhabited by dead and empty shells; the community structure is likely to be different. For example, the motile nature of hermit crabs likely to inhibit the presence of sedentary polychaetes (Chapter 2). It is interesting to note that while the presence of dead and empty screwshells may result in an increase in hermit crab densities by several 100 m^{-2} (Reid 2003), there is no evidence of a change in oxygen flux that might be attributed to respiration of the hermit crabs (Chapter 3). The reason(s) behind this paradox remains unclear and warrants further investigation.

This spatial and temporal variability in impacts are also likely to be extended to commercially important scallops (*Pecten fumatus*). *Maoricolpus roseus* negatively impacted *P. fumatus* distribution, growth and condition (Chapter 3, Chapter 4). The impact of *M. roseus* on *P. fumatus* was evident at even moderate screwshell densities (200 m^{-2}), where soft-sediment habitat occupied by screwshells at or above this density were effectively rendered as uninhabitable by *P. fumatus*. Importantly, the impact of *M. roseus* was similar for both living and dead and empty shells, indicating that the loss of habitat available to *P. fumatus* due to its occupancy by *M. roseus* is an impact likely to be long in duration. Given that *M. roseus* now occupies

potentially vast expanses of seafloor, a very large area of previously viable scallop habitat is now occupied by *M. roseus* at densities high enough to significantly impact *P. fumatus*. However, it is noted that extrapolation of results obtained in small-scale manipulative experiments to larger spatial and temporal resolution is potentially fraught with problems (Thrush et al. 1997a, Thrush et al. 1997b, Thrush et al. 1997c), particularly when the species is an ecosystem engineer (Hastings et al. 2007). Therefore, the previous description of potential spatial and temporal variability in impacts of *M. roseus* clearly includes a degree of inherent speculation, and I acknowledge the concept warrants further investigation.

6.4 MANAGEMENT OPTIONS FOR M. ROSEUS

Given the magnitude of impact of *M. roseus* on native communities and *P. fumatus*, there is clearly a need to implement a management strategy to minimize the risk of further spread of this species. Minimizing further spread is an immediate pragmatic option, while eradication it is certainly not a viable option for this species given that it now occupies such a vast area at high densities. The most feasible and economically viable strategy would include mitigation measures to ensure that the species does not expand westward into South Australia and south Western Australia. The reproductive ecology, dispersal and invasive nature of the species have allowed its expansion northward into the south eastern corner of the Australian mainland, probably aided by northwards flowing countercurrents to the southward East Australian Current. In this context, Australia is fortunate that major ocean currents in southern Australia largely flow west-to-east, which is unfavorable for the transport of *M. roseus* larvae westward, and ostensibly the principal reason why *M.*

roseus has not already ventured into the western states of Australia. Arguably, the greatest risk of westward dispersal of *M. roseus* is by anthropogenic vectors. Given the large amount of international and domestic commercial vessel traffic, and a high amount of unchecked recreational boating, the potential for the westward transportation of viable *M. roseus* propagules is relatively high, especially given the relatively long larval phase of the species. It would be prudent to develop or enhance existing guidelines, policy and legislation to ensure westward transfer of *M. roseus* propagules is minimized.

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